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ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM

A Review and Assessment of the Baseline Data Relevant to the Impacts of Oil Sands Development on Large Mammals in the AOSERP Study Area

Project LS 21.6.1
April 1980

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ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM RESEARCH REPORTS

These research reports describe the results of investigations funded under the Alberta Oil Sands Environmental Research Program, which was established by agreement between the Governments of Alberta and Canada in February 1975 (amended September 1977). This 10-year program is designed to direct and co-ordinate research projects concerned with the environmental effects of development of the Athabasca Oil Sands in Alberta.

A list of research reports published to date is included at the end of this report.

Enquiries pertaining to the Canada-Alberta Agreement or other reports in the series should be directed to:

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A Review and Assessment of the Baseline Data Relevant to the Impacts of Oil Sands Developments on Large Mammals in the AOSERP Study Area

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AOSERP Report 64

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The Hon. John W. (Jack) Cookson
Minister of the Environment
222 Legislative Building
Edmonton, Alberta

and

The Hon. John Roberts
Minister of the Environment
Environment Canada
Ottawa, Ontario

Sirs:

Enclosed is the report "A Review and Assessment of the Baseline Data Relevant to the Impacts of Oil Sands Developments on Large Mammals in the AOSERP Study Area".

This report was prepared for the Alberta Oil Sands Environmental Research Program, through its Land System, under the Canada-Alberta Agreement of February 1975 (amended September 1977).

Respectfully,

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Chairman, Steering Committee, AOSERP
Deputy Minister, Alberta Environment

A.H. Macpherson, Ph.D.
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A REVIEW AND ASSESSMENT OF THE BASELINE DATA RELEVANT TO THE IMPACTS OF OIL SANDS DEVELOPMENTS ON LARGE MAMMALS IN THE AOSERP STUDY AREA

DESCRIPTIVE SUMMARY

BACKGROUND

Large mammals (woodland caribou, moose, and wolves), because of their high public profile, were one of the areas identified initially for investigation when the Alberta-Canada agreement created AOSERP in 1975. Research at that time focused selectively on determining basic population parameters such as density, mortality, habitat preferences, seasonal movements, and population dynamics.

With the completion of these baseline projects, program management, pursuing a policy of assessment and evaluation, commissioned an external review of the data generated. The objective of this review was two-fold:

1. To conduct a detailed review of current literature and;
2. To provide an assessment and evaluation of the data generated under AOSERP funding based on its applicability to the assessment of the potential impact that the development of the Athabasca Oil Sands would have on large mammals.

ASSESSMENT

The final report, "A Review and Assessment of the Baseline Data Relevant to the Impacts of Oil Sands Development on Large Mammals in the AOSERP Study Area", prepared by D.C. Thompson, D.M. Ealey, and K.H. McCourt of McCourt Management, has been reviewed by scientists at the University of Alberta and within the governments of Alberta and Canada. As a result of these reviews, Program Management of AOSERP accepts this final report and recommends that it be published and receive wide distribution. Program management would like to extend their appreciation to the authors for their contribution to the program data base.

W.R. MacDonald
Director (1980-81)
Alberta Oil Sands Environmental
Research Program

A REVIEW AND ASSESSMENT OF THE BASELINE DATA RELEVANT TO THE IMPACTS OF OIL SANDS DEVELOPMENTS ON LARGE MAMMALS IN THE AOSERP STUDY AREA

by

D.C. THOMPSON, D.M. EALEY, AND K.H. McCOURT
McCourt Management Ltd.

for

ALBERTA OIL SANDS ENVIRONMENTAL
RESEARCH PROGRAM

Project LS 21.6.1

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ABSTRACT

The available baseline data which are relevant to the documentation and evaluation of the impacts on large mammals (moose, woodland caribou, wolf) which would result from oil sands development are reviewed. An approach to the analysis of impacts was developed to provide a logical framework for the determination of what types of baseline data were relevant to the objectives of study. Baseline data for each species were discussed under three categories: seasonal population dispersion, the potential impacts of large development projects, and population dynamics. The review forms the basis of the evaluation of the state of baseline knowledge of large mammals in the AOSERP study area and a statement of the research which should be completed in order to provide the data.

A critique of the state of the baseline knowledge of large mammals (moose, woodland caribou, wolf) was conducted with the objectives being to determine whether or not baseline knowledge of these species is adequate to assess the impacts of large developments on large mammal populations in the AOSERP study area, and to identify specific knowledge gaps.

Major gaps in the baseline knowledge of moose were: seasonal habitat use, the effects of sensory disturbances and population density; a minor gap was identified in the knowledge of the effects of development on direct mortality of moose.

Major gaps in the baseline knowledge of woodland caribou were: distribution on the AOSERP study area, seasonal habitat use, the effects of sensory disturbance, and population density; minor gaps were identified in the knowledge of the effects of development on direct mortality of woodland caribou.

Major gaps in the baseline knowledge of wolf were: seasonal habitat use and population density; minor gaps were identified in the knowledge of the seasonal movement patterns, the effects of sensory disturbances, and the effects of development projects on direct mortality of wolves.

ACKNOWLEDGEMENTS

This research project LS 21.6.1 was funded by the Alberta Oil Sands Environmental Research Program, a joint Alberta-Canada research program established to fund, direct, and co-ordinate research into the effects of oil sands development on the renewable resources of the Athabasca Oil Sands.

1. INTRODUCTION

Three of the tenets upon which the Canada-Alberta agreement for the Alberta Oil Sands Environmental Research Program (AOSERP) is founded are:

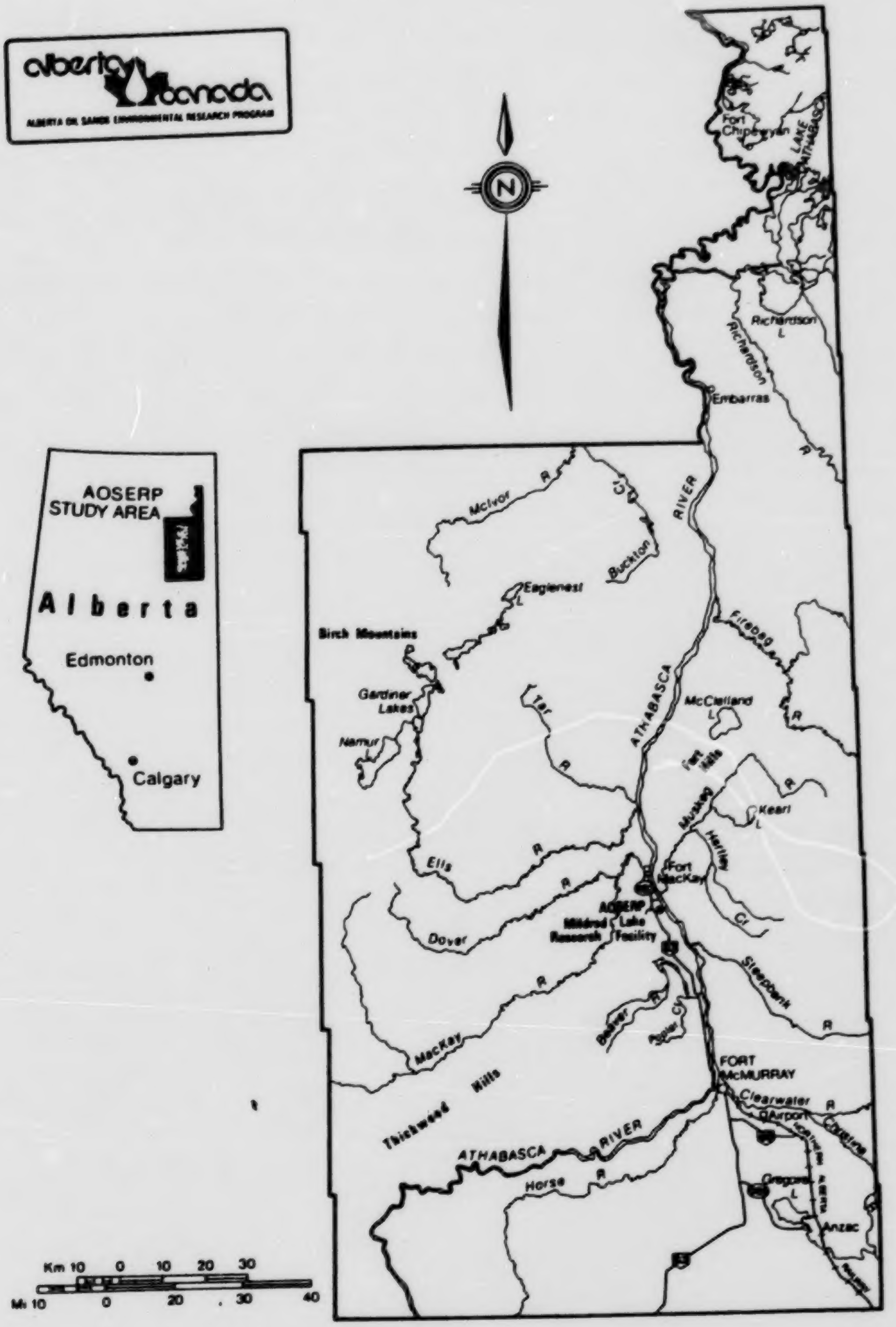
1. Canada and Alberta recognize the necessity of improving the scientific understanding of the *effects of the oil sands development* on human and natural environment of the AOSERP study area.
2. The results of an intensive study of the area will be useful in *predicting the effects of any proposed development* as a basis for considering future proposals.
3. The results of the study program will be utilized by Alberta in the approval process for future developments and in the environmental design of any project which might be implemented.

It is clear, therefore, that AOSERP was established with at least two major goals in mind:

1. To conduct research which will be useful in predicting the environmental effects of oil sands developments, and
2. To conduct research which will provide an understanding of the environmental effects of development such that this knowledge may be used in the environmental design of future developments.

Development of the Athabasca Oil Sands will affect large mammals (moose, caribou, and wolf) to varying degrees through alteration of habitat, disturbance factors, and increased exploitation. Large mammal research in the AOSERP study area (Figure 1) was initiated in 1975 and continued to the present date under several projects. Research emphasis from 1975-78 has been on establishing baseline states for large mammals. The general objective of this project is to complete an analysis of the applied research necessary to allow evaluation of the effects of oil sands development on large mammals.

This objective has been fulfiled in two basic stages: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Ells R
Fort MacKay
AOSERP Mildred Lake Research Facility
Dover R
Steepbank R
MacKay R
Beaver R
Poplar Cr
FORT McMURRAY
Clearwater R
Airport
Christina
Thickwood Hills
ATHABASCA RIVER
Horse R
Gregoire L
Anzac
Km 10 0 10 20 30
Mi 10 0 20 30 40

Figure 1. Location of the AOSERP study area.

(1) a review of the available baseline data which is relevant to an assessment of the effects of development on large mammals in the AOSERP study area; and (2) an evaluation of the adequacy of available baseline data and an identification of data gaps which remain.

The objective of this report is to review and to provide an evaluation of the adequacy of the available baseline data which are relevant to the documentation and evaluation of the impacts on woodland caribou, moose, and wolves (large mammals) which would result from oil sands development in the AOSERP study area.

1.1 APPROACH TO IMPACT ANALYSIS

In order to determine what baseline data are relevant to the documentation and evaluation of impacts on large mammals, it is necessary to adopt an approach which provides a logical framework for the analysis of impacts.

The ultimate goal of any environmental impact assessment is to provide the information necessary to determine whether the structural and functional integrity of ecosystems in the vicinity of the proposed development is threatened. An environmental impact assessment involves two main stages: (1) the documentation of the impacts which will occur; and (2) the evaluation of the significance of those impacts.

1.1.1 Documentation of Impacts

An environmental impact may be defined as a change in a component of the natural environment (i.e., a large mammal population) which was induced by an unnatural environmental component (i.e., oil sands development). The documentation of environmental impacts, therefore, involves a description of a development project's components, a description of those environmental components that will be involved in interactions with the project's components, and an estimation of the magnitude of those changes in the environmental components that will result from interactions with the project.

In order to determine if any interaction will occur, the distribution of each species, in relation to the project, must be known; the frequency of interactions will be dependent upon the density of each species in the area subject to development.

Interactions between large mammals and development projects may be either indirect or direct (Figure 2). Indirect interactions occur through the alteration of habitats available to the population. Habitat alterations may take the form of alteration of the vegetation of an area, ranging from the complete destruction of habitat (e.g., strip-mined land) to the alteration of the vegetational characteristics of the habitat (e.g., brush clearing); habitat alterations may also take the form of a change in the structural characteristics of the habitat (e.g., construction of a road). The net result of such habitat alterations will be to alter the carrying capacity of the range. High quality habitat will generally provide either more or higher quality food and cover than will low quality habitat; therefore, higher quality habitat will typically support ("carry") greater densities of animals than will low quality habitat. Hence, alteration of habitat by a development project will ultimately affect the size of wildlife populations.

The magnitude of the effect which a given habitat alteration will produce on wildlife populations depends upon the relative amount and quality of the habitat altered and whether the alteration is detrimental or beneficial to the wildlife population in question. Therefore, the magnitude of the change in wildlife populations which will result from the alteration of habitat by an industrial project may be estimated from a knowledge of the seasonal wildlife habitat selection patterns, particularly the proportion of time which is spent by the population in each of the available habitat types during each season (seasonal density).

Direct interactions between wildlife populations and development projects may occur in two ways: (1) sensory disturbances; and (2) direct mortality. Continuous, intolerable sensory disturbances (e.g., continuous loud noise) may produce a reduction of the carrying capacity of the area because of the passive

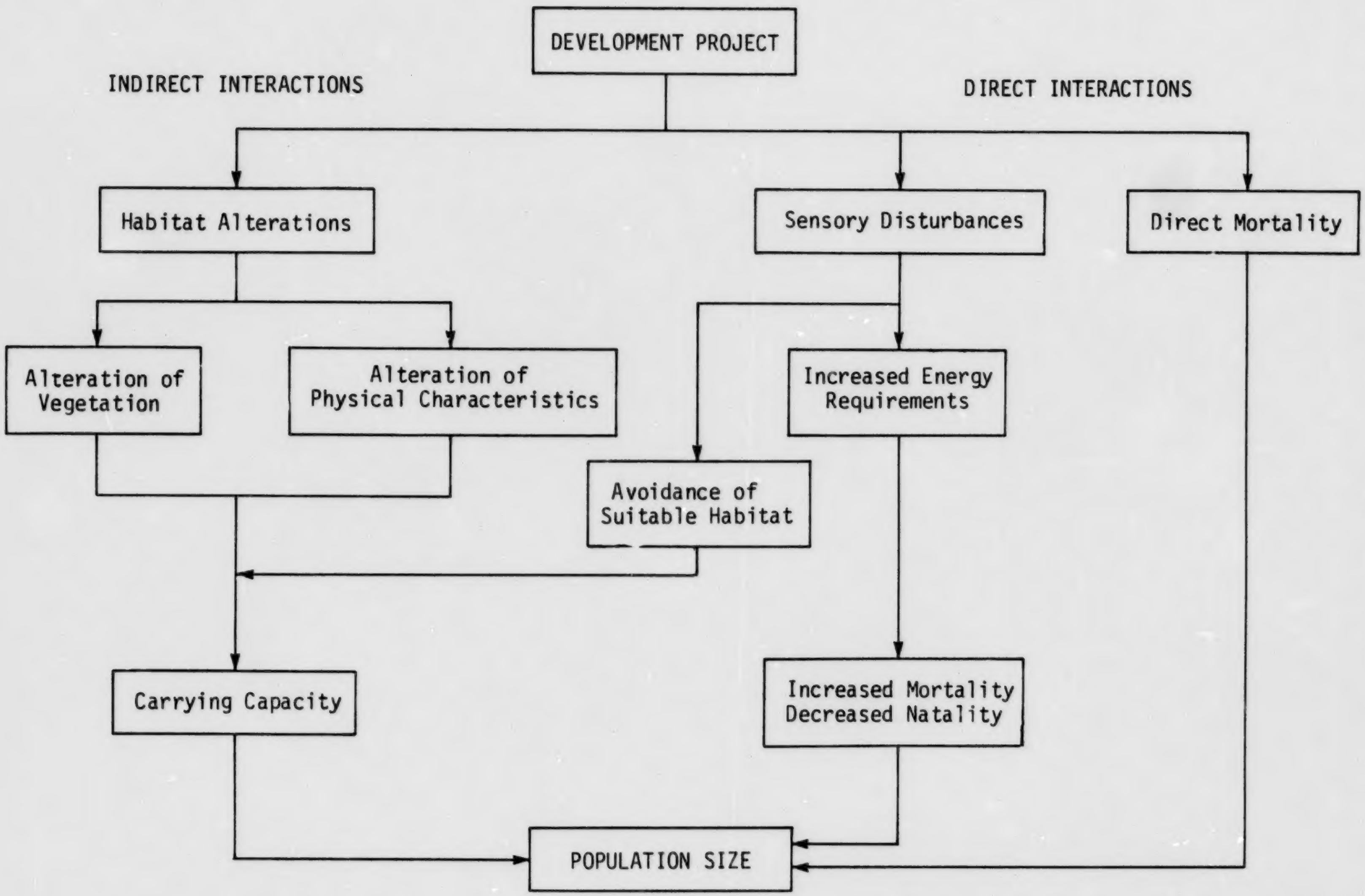
DEVELOPMENT PROJECT
INDIRECT INTERACTIONS
DIRECT INTERACTIONS
Habitat Alterations
Sensory Disturbances
Direct Mortality
Alteration of Vegetation
Alteration of Physical Characteristics
Increased Energy Requirements
Avoidance of Suitable Habitat
Carrying Capacity
Increased Mortality Decreased Natality
POPULATION SIZE

Figure 2. A conceptual approach to the documentation of the impacts of development projects on wildlife populations.

avoidance of suitable habitat by wildlife. Active avoidance of intolerable discontinuous sensory disturbances (e.g., aircraft overflights) will result in increased energy expenditure. The effects of an increased expenditure of energy may be manifested in increased mortality of individuals through starvation, predation, disease, etc., or in a decreased production of young through a decrease in pregnancy rates, increased abortions or absorbtion of embryos, and decreased likelihood of survival of young. Active avoidance of sensory disturbances may also result in injuries causing deaths. Direct mortality of wildlife may also result from causes such as collisions with vehicles, poisoning, accidents, and hunting. Therefore, sensory disturbances to, and direct mortality of wildlife which is induced by a development project will ultimately affect the size of wildlife populations.

The change in population size which will result from habitat avoidance will depend on the amount of habitat avoided, the season and duration of avoidance, and the number of animals normally dependent upon the habitat which is avoided. The numbers of animals which undergo stress reactions to sensory disturbances or are killed or injured by collisions with vehicles will depend upon the density of animals expected to be in the vicinity of disturbances and the types and magnitude of disturbances which are produced by the specific development project.

It is evident, therefore, that two major types of baseline data are required to enable documentation of the impacts which any development project will produce on large mammal populations: (1) a knowledge of the seasonal population dispersion (distribution, habitat use, and movements) in relation to the proposed project; and (2) a knowledge of the susceptibility of wildlife species to disturbances (sensory disturbances, habitat alterations) produced by the proposed project.

We anticipate that the most significant impacts which oil sands development will have on large mammal populations will be those resulting from habitat loss or alteration; this will include habitat made unuseable by terrain alterations and intolerable sensory disturbance. Therefore, a knowledge of the seasonal density of each species of large mammal within each of the habitat types on the AOSERP study area and of the sphere of influence of various types of sensory disturbance are considered to be the most critical data required to allow documentation of the impact of oil sands developments on large mammals.

1.1.2 Evaluation of Impacts

Once the impacts produced by a development project have been documented, their significance must be evaluated. The most meaningful and practical way to evaluate environmental impacts on large mammals is to consider the magnitude and duration of changes in population numbers.

Not all changes in population size are reasons for concern. Natural fluctuations in population size occur within each year as a result of mortality of some animals and production of young, and between years as a result of the imbalance between mortality and recruitment. As populations and ecosystems are adapted to these natural changes in population size, their structural and functional integrity is not threatened by changes of the magnitude and duration that they experience under natural conditions. Therefore, changes in population size induced by man's activity which do not increase the amplitude of population fluctuations beyond their natural limits can be considered of minor significance to populations and ecosystems; major impacts are those which do increase population fluctuations beyond their natural limits.

To determine whether an impact on an animal population is likely to be major or minor, the expected magnitude and duration of population change must be compared with the population dynamics of the population. A minor impact on a species characterized by a high reproductive potential and large fluctuation in population levels could involve a much greater proportion of the population than a minor impact on a species characterized by a low reproductive potential and small fluctuations in population levels.

It is evident, therefore, that a knowledge of natural fluctuations in population levels, which can include a knowledge of aspects of population dynamics, such as the annual recruitment and mortality rates and the reproductive potential, is essential in the evaluation of impacts produced by any project. Therefore, this report will review the current state of knowledge of population dynamics of woodland caribou, moose, and wolf; these data are required to allow an evaluation of impacts produced by any oil sands development which may occur on the AOSERP study area.

2. REVIEW OF BASELINE DATA RELEVANT TO LARGE MAMMALS IN THE AOSERP STUDY AREA

2.1 OBJECTIVES

The specific objectives of this section are to review the literature on large mammals relevant to an evaluation of the responses of woodland caribou, moose, and wolves to oil sands development. Therefore, the topics which will be reviewed are:

1. Dispersion of large mammals in relation to their habitat;
2. The potential impacts of large development projects on large mammals; and
3. The population dynamics of large mammals.

Special emphasis will be given to review of studies conducted on the AOSERP study area.

3. WOODLAND CARIBOU

Five geographical subspecies of caribou are currently recognized in Canada: the woodland caribou (*Rangifer tarandus caribou*), which occupies the boreal forest region of southern Canada from Newfoundland and Labrador to British Columbia and as far north as treeline in the Northwest Territories and approximately the Ogilvie Mountains in the Yukon; the Grant caribou (*R. t. granti*), which occupies the northern Yukon; the barren-ground caribou (*R. t. groenlandicus*), inhabiting the continental tundra zone in the Northwest Territories as well as Baffin and Bylot Islands; the Peary caribou (*R. t. pearyi*) of the Queen Elizabeth Islands; and the introduced European reindeer (*R. t. tarandus*) in the Mackenzie Delta area (Banfield 1974).

The subspecies of caribou which occurs in the AOSERP study area is the woodland caribou. Although the woodland caribou differs from other caribou in its year-long use of forested habitat, it is considered most likely that the population processes of woodland caribou are similar to those of other caribou.

3.1 SEASONAL POPULATION DISPERSION

Two main topics must be discussed to gain a knowledge of the seasonal population dispersion of woodland caribou: seasonal distribution in relation to habitat and seasonal movements.

3.1.1 Seasonal Distribution in Relation to Habitat

Habitat selection of woodland caribou is related to their requirements for food and shelter and is strongly influenced by snow conditions (Fischer et al. 1977a).

3.1.1.1 Winter habitat use. Most investigators generally agree that terrestrial and arboreal lichens are the species most heavily used by caribou in winter (Simkin 1965; Ahti and Hepburn 1967; Bergerud 1972). Terrestrial lichens, primarily of the genera *Cladonia* and *Cetraria*, are considered by most authors to constitute the bulk of the winter diet (Hustich 1951; Cringan 1956; Ahti 1959; Simkin 1960, 1965; Ahti and Hepburn 1967; Burgess 1970). In southern locations, arboreal lichens (*Usnea* spp., *Alectoria* spp., *Evernia* spp.) are also heavily used (Cringan 1956, 1957; Evans 1960; Edwards and Ritcey 1960; Edwards et al. 1960; Freddy 1974; Stelfox et al. 1978). Ahti and Hepburn (1967) note that in areas of Ontario where both terrestrial and arboreal lichens are abundant, the terrestrial lichens are heavily used while the arboreal lichens are left untouched. Bergerud (1972) reported that woodland caribou in Newfoundland fed heavily on terrestrial lichens in fall; however, as the snow depth increased the caribou fed increasingly on the more accessible arboreal lichens. Other authors have commented on the use of arboreal lichens by caribou when terrestrial lichens are either absent or inaccessible due to snow cover (Dugmore 1913; Formozov 1946; Hustich 1951; Edwards et al. 1960; Sulkava and Helle 1975). Reindeer herders have occasionally cut down lichen covered trees to augment the diet of their herds during critical winter periods (Llano 1944).

Despite the heavy use by caribou, lichens are relatively low in nutrient quality (Courtright 1959; Kelsall 1968; Skoog 1968). Feeding trials conducted by Palmer (1944), Kennedy and Titus (*in* Courtright 1959), Ahti (*in* Kelsall 1968) and Bergerud (1974a) suggest that lichens alone do not provide an adequate diet for reindeer or caribou, although they can subsist on them for long periods (Kelsall 1968). Compared to lichens, most vascular species are high in nutrient quality (Kelsall 1968). Thus, most workers consider that green vegetation in winter is essential to the well being of caribou (Karev 1961; Zhigunov 1961; Ahti and Hepburn 1967; Skoog 1968).

In winter, the Cyperaceae genera *Carex* and *Eriophorum* maintain green shoots within the dry leaf-sheath. Sedges, where available, are readily consumed by woodland caribou in winter (Edwards and Ritcey 1960; Simkin 1965; Brokx 1966; Burgess 1970; Bergerud 1972; Schmidt 1977). Stelfox et al. (1978) report that caribou in Jasper feed primarily on lichens in winter, although the use of graminoids was also evident; this pattern has also been reported in Norway (Gaare and Skogland 1971). In the Peace-Athabasca Delta, Kelsall (1970) witnessed caribou digging out and devouring the contents of muskrat feeding lodges, which contained mostly sedges.

Browse species also appear to be important sources of winter green-feed to caribou. Evergreen shrubs such as *Ledum* spp. and other vasculars which have green wintering leaves and shoots (*Vaccinium* spp., *Arctostaphylos* spp., *Cornus* spp., *Linnaea* spp., *Equisetum* spp., *Abies* spp.) are readily consumed by caribou in winter (Edwards and Ritcey 1960; Skunke 1963; Simkin 1965; Brokx 1966; Burgess 1970; Bergerud 1972, 1974a; Freddy 1974; Stelfox et al. 1978). Bergerud (1974a) reports some caribou in Newfoundland which were living mostly on balsam fir (*Abies balsamea*).

Most authors consider that mosses are eaten only incidentally (Palmer 1926; Banfield 1954; Skoog 1956, 1968; Stelfox et al. 1978). However, Bergerud (1972) reports that mosses comprised 6% of the winter diet of woodland caribou in Newfoundland. Skoog (1968) suggests that mosses may be an emergency-type food, eaten when other food species are unavailable.

Forbs do not appear to be heavily used by caribou during winter (Cringan 1956; Evans 1960).

In summary, the winter diet of the woodland caribou appears to consist primarily of either terrestrial or arboreal lichens, or both. However, there is ample evidence that caribou use vascular species as sources of green-feed throughout the winter. Thus, good winter caribou range must supply quantities of terrestrial and/or arboreal lichens as well as sources of winter green-feed, such as evergreen shrubs or sedges. No specific data are available concerning the winter diet of woodland caribou in the AOSERP study area; however, it is unlikely that any major variation exists between the species taken by woodland caribou in the AOSERP study area and in other boreal forest areas.

Snow and its effect on forage availability is a major factor in determining the use caribou will make of available range in winter (Bergerud 1971a; D.R. Miller 1974; Stardom 1975).

Woodland caribou are first found in areas which contain suitable forage and then react to the various snow conditions within this winter range (Edwards 1956; Stardom 1975). Thus, burned habitats have been shown to be unsuitable as winter range for caribou, primarily because of the lack of forage, principally lichens (Leopold and

Darling 1953 a, b; Edwards 1954; Cringan 1956, 1957; Evans 1964; Peterson 1966; Scotter 1964, 1967). Similarily, deciduous forest is likely unsuitable to woodland caribou because of the lack of suitable forage (Fischer et al. 1977a). Areas of suitable winter range are generally considered to be located primarily in open mature conifer stands and muskegs (Cringan 1956, 1957; Simkin 1965; Ahti and Hepburn 1967; Fischer et al. 1977a, Euler et al. 1976; Schmidt 1977). Areas of closed, dense conifers appear to contain less lichen forage and are less attractive to caribou than are areas of open conifers (Ahti and Hepburn 1967).

As feeding craters appear to be dug only when caribou are aware that food is present, the suitability of winter range for feeding is related to the frequency with which caribou may make contact with food through the snow (Bergerud 1971a, 1974b). It has been shown that caribou are better able to detect food through soft snow than through dense snow, and through thin snow better than through thick snow (Bergerud 1974b). Pruitt (1959) stated that ideal snow conditions for caribou in forested habitats should have a hardness of less than 60 g/cm^2, a density not greater than 0.20 and a depth of less than 60 cm. Varied topography and vegetation cover will alter wind speeds and thereby affect the depth and density of snow. Thus, Bergerud (1974b) has suggested that the taiga range, which presents woodland caribou with the best feeding opportunities, should not have trees which are spaced too closely, which allows the accumulation of deep, soft snow, or too widely, which results in the formation of hard, wind-packed snow. Bergerud (1974b) suggests that optimum winter feeding range for woodland caribou will be of varied terrain, and will contain lichens, shrubs, and scattered trees, but no closed canopy forests. D.R. Miller (1974) showed that as snow depth increases and as crusts are formed on exposed sites, caribou will forage primarily in treed areas, especially in semi-open conifer stands. Stardom (1975) noted that woodland caribou fed mainly in open bogs until the snow cover approached 60 cm in depth and had a crust hardness of 400 g/cm^2; caribou then moved to mature jackpine forest where both snow depth and hardness were less. Stelfox et al. (1978) have shown that in January and February, caribou in the alpine-tundra regions of Jasper sought areas with thin or no snow cover. Schmidt (1977) indicated that open conifer stands (10-20% cover) received heavier use than more closed stands (greater than 50%).

Despite their forest-dwelling habits, woodland caribou seem to have an affection for open situations. Brokx (1966) considered that this affection may be due to the recent evolution of the forest-dwelling habits, which presumably occurred during the last glaciation (Banfield 1961). This affection for open areas is likely due to the fact that snow conditions in open areas, such as lakes and fens, are more conducive to loafing and travel than are those of the adjacent forest (Pruitt 1959; Brokx 1966; McCourt et al. 1974a; Stardom 1975). Although the soft snow conditions of open coniferous stands are well suited for feeding, they restrict mobility. Edwards and Ritcey (1959) described woodland caribou sinking to their chests in deep, soft snow. The deep snow of mountainous regions appears to trap caribou annually in valley bottoms, until the snow becomes firm enough to travel (Edwards and Ritcey 1960; Edwards et al. 1960). Pruitt (1961) suggested that caribou use open areas as escape, travel, and loafing habitat. Surrendi and DeBock (1976) indicate that caribou in open terrain are less susceptible to surprise attack by predators than those in forest cover. Brokx (1966) and Ruttan (1960) have noted that open treeless areas with boreal forest, such as fens, are extensively used by woodland caribou for winter travel. Loughrey (*in* Brokx 1966) stated that caribou sleep and rest more frequently in open areas than in unbroken stretches of forest. Ruttan (1960) notes that open areas are used by caribou for loafing.

The availability of open escape and loafing cover appears to restrict the use of available range by caribou. D.R. Miller (1974) noted it was conspicuous that caribou concentrated on the use of forage supplies close to open areas; little use appeared to be made of forage supplies further than 1 km from open areas. Brokx (1966) also pointed out that caribou tend to feed along the edges of bogs and fens, sites which were removed from these open areas being inaccessible because of unfavourable snow conditions. Schmidt

(1978) indicated that open habitats such as fens, rivers, creeks, and lakes were consistently used by woodland caribou for bedding, loafing, and travel and only occasionally for feeding; upland forested areas were consistently used for feeding and only occasionally for bedding.

Therefore, it appears that two distinct types of cover must be present to provide winter range which is of value to woodland caribou: areas of open, mature coniferous forest (containing appropriate forage), and interspersed open areas. The open coniferous areas provide food and cover, while the open areas provide avenues of escape and travel.

Ideal woodland caribou habitat appears to be the complexes of open mature muskeg interspersed with fens and lakes. Many authors have noted the affinity of woodland caribou for such habitat. Swanson et al. (*in* Cringan 1956) noted that the last herd of woodland caribou in Minnesota frequented open muskegs during the winter. Ruttan (1960) reported that feeding of woodland caribou in Saskatchewan was confined to open spruce, tamarack, and muskegs; during studies in both Saskatchewan and in the Mackenzie River basin Ruttan (*in* Pendergast et al. 1974) noted that caribou made extensive use of grassy fens for loafing and travel. Brokx (1966) showed that raised bogs interspersed with sedge fens were the preferred winter habitat of woodland caribou in the Hudson Bay Lowlands. Burgess (1970) observed that woodland caribou in Alberta are commonly found in open muskeg situations. The winter range of the Humber River herd, Newfoundland, is largely bogs with some open lichen woodland (Bergerud 1971a). Open tamarack bogs and mature coniferous ridges are the most important winter habitats of woodland caribou in southeastern Manitoba with lakes being used for loafing and travel (Stardom 1975). The muskeg-fen complex is the habitat type most heavily used by woodland caribou in northeastern Manitoba and northwestern Ontario (Fischer et al. 1977a).

3.1.1.2 Winter habitat use by woodland caribou in the AOSERP study area. Data which are available concerning the winter habitat use of woodland caribou in the AOSERP study area generally agree with those from other portions of the woodland caribou range. A total of 405 relocations of radio-collared woodland caribou were made by Fuller and Keith (in prep. a) during the period November to March; 63.4 percent of all relocations were from lowland areas, with 75 percent of all lowland observations being from the black spruce-muskeg habitat type. Open muskeg and unburned, mature black spruce were the other important lowland habitat types. Feeding activities were observed disproportionately more often in open and black spruce muskegs than in the other available habitats (Fuller and Keith in prep. b). However, Fuller and Keith (in prep. a) state that the winter habitat relationships for woodland caribou on the AOSERP study area may not be well defined due to a lack of significant snow cover during the winter of 1977.

3.1.1.3 Summer habitat use. Relatively little quantitative data exist concerning the summer habitat use of woodland caribou; however, it is generally held that, as in winter, the summer habitat selection of woodland caribou depends, at least in part, on the summer food habits.

The summer diet of woodland caribou appears to be less restricted than the winter diet and is characterized by graminoids, herbs, and deciduous shrubs; however, lichens also appear to be important constituents of the summer diet. The shift from winter foods to summer foods is, therefore, basically a shift from a dependence on nonvascular (lichen) to vascular vegetation. The change between these must necessarily be a gradual one to allow time for the adaptation of the rumen flora.(Brokx 1966; Ahti and Hepburn 1967). In general, the importance of lichens declines as the snow disappears and the green vegetation appears. Simkin (1965) shows that lichens are much more important in May and June (60.4% of total) than in July (35.2% of total).

A wide variety of graminoids are eaten by woodland caribou during summer; however, sedges, particularly *Carex* spp. and

Eriophorum spp., appear to be preferred over grasses (Edwards and Ritcey 1960; Simkin 1960, 1965; Brokx 1966; Ahti and Hepburn 1967; Schmidt 1977). Stelfox et al. (1978) have shown that 18.4 percent of the May-October diet of woodland caribou consists of graminoid species; 16.2 percent of the May to October diet consists of *Carex* spp. In July, 34.8 percent of the total woodland caribou diet consisted of graminoids; 31.6 percent of this total consisted of *Carex* spp.

A wide variety of large shrubs and trees have been reported to be taken by woodland caribou in summer. Cringan (1956) indicates that willows (*Salix* spp.) highbush cranberry (*Viburnum rafinesquiana*), bush honeysuckle (*Diervilla lonicera*), trembling aspen (*Populus tremuloides*), salmon berry (*Rubus parviflorus*), red-osier dogwood (*Cornus stolonifera*), and raspberry (*Rubus* spp.) were among the trees and large shrubs utilized on the Slate Islands. In Wells Gray Park, huckleberry (*Vaccinium membranaceum*), dwarf huckleberry (*Vaccinium caespitosum*), boxwood (*Pachystima myrsinites*), and willow (*Salix* spp.) were used. Bog-birch (*Betula pumila*), white birch (*Betula papyrifera*), trembling aspen, balsam poplar (*Populus balsamifera*), and several species of willows (*Salix pedicellaris, S. planifolia, S. bebbiana,* etc.) were the trees and large shrubs which were important to woodland caribou in Ontario (Ahti and Hepburn 1967). Simkin (1965) indicates that trees and tall shrubs comprise 51 percent of the July diet of woodland caribou at Irregular Lake, Ontario. White birch, trembling aspen, and pin cherry (*Prunus pensylvanica*) provided 13.6 percent, 12.8 percent, and 9.6 percent respectively, of the July diet (Simkin 1965). Willows, juneberry (*Amelanchier* spp.), and alder (*Alnus crispa*) are other tall shrubs used in summer (Simkin 1965). During the spring, the buds and twigs of trees and tall shrubs were browsed by woodland caribou; later in the summer, only the succulent leaves were eaten (Simkin 1965). Stelfox et al. (1978) have shown that tall shrubs and trees comprised 18.5 percent and 27.7 percent of woodland caribou diet during July and August, respectively. Willows were the tall shrub and tree species most used by woodland caribou, with fir (*Abies lasiocarpa*), spruce (*Picea* spp.), juniper (*Juniperus* spp.), and buffaloberry (*Shepherdia canadensis*) being used only sparingly.

A wide variety of herbs and low shrubs have been reported in the summer diet of woodland caribou. Simkin (1965) reports that herbs and low shrubs comprised 13.6 percent of the July diet of woodland caribou at Irregular Lake, Ontario. The major herb and low shrub species reported to be taken were: Labrador tea (*Ledum groenlandicum*), elder (*Aralia hispida, A. racemosa*), gooseberry (*Ribes* spp.), blueberries (*Vaccinium angustifolium, V. myrtilloides*), raspberry (*Rubus* spp.), rose (*Rosa* spp.), dogwood (*Cornus stolonifera*), horsetail (*Equisetum* spp.), yellow loosestrife (*Lysimacachia terrestria*), marsh-marigold (*Caltha palustris*), milk vetch (*Astragalus alpinus, A. eucosmus*), bogbean (*Menyanthes trifoliata*), louseworts (*Pedicularis* spp.), coltsfoot (*Petasites* spp.), and fireweed (*Epilobium angustifolium*) (Simkin 1965; Ahti and Hepburn 1967). Stelfox et al. (1978) indicate that herbs and low shrubs comprise 3.4 percent and 8.6 percent of the July and August diet, respectively, of woodland caribou. The major herb and low shrub species included in the summer diet were wormwood (*Artemisia* spp.), milk vetch (*Astragalus* spp.), a variety of ericaceous shrubs, twin flower (*Linnaea borealis*), *Potentilla* spp., various composites, avens (*Dryas* spp.), and horsetails (*Equisetum* spp.). The leguminous species, which are generally high in proteins, seem to be especially preferred among vascular plants. Their high palatability has been mentioned by several authors (Shelford and Olsen 1935; Vassiliev 1936; Murie 1944; Banfield 1954; Andreev 1957).

Despite the fact that green, vascular vegetation characterizes the summer diet, woodland caribou are also known to utilize lichens to a significant degree in summer (Cringan 1956, 1957; Simkin 1960, 1965; Ahti and Hepburn 1967). Simkin (1965) indicates that terrestrial lichens of the genus *Cladonia* comprised 24.8 percent of the total diet of woodland caribou in July; arboreal lichens (*Usnea* spp., *Evernia* spp., *Alectoria* spp., *Parmelia* spp.) composed 10.4 percent of the July diet of woodland caribou. Stelfox et al. (1978) show that lichens of the genera *Cetraria*, *Cladonia*, and *Peltigera* comprise 28.6 percent and 27 percent of the diet of the woodland caribou in July and August, respectively.

No specific data are available concerning the summer diet of woodland caribou from the AOSERP study area; however, it is unlikely that any major difference exists between foods of woodland caribou on the AOSERP study area and in other boreal forest areas.

In spring and summer, woodland caribou tend to prefer low, marshy areas to the uplands (Brokx 1966; Loughrey 1957; Schmidt 1977). Sites such as fens and drainageways contain abundant sedge and forb vegetation mixed with low shrubs which, together, provide the majority of the foods taken. Ahti and Hepburn (1967) consider eutrophic sedge fens to be excellent summer range for woodland caribou. Stelfox et al. (1978) have also shown that woodland caribou concentrate on lake deltas in spring to feed on new growths of grasses and sedges.

Well-drained sites, particularly beaches or drumlins, that become free of snow in early spring are favoured by woodland caribou as calving areas (Brokx 1966; Loughrey 1957; Schmidt 1977). Preferable calving grounds have fairly regular topography, with a minimum of deadfall, a good food supply, good visibility, and good conifer cover (Simkin 1965).

Open muskeg areas appear to be more heavily used in summer than the upland types (Schmidt 1977; Fuller and Keith in prep. a); Ahti and Hepburn (1967) consider that most black spruce muskegs produce considerable amounts of summer food.

Several authors have noted that old burns may provide the forb-grass-shrub regeneration that serves as summer food for woodland caribou (Brokx 1966; Schmidt 1977).

In areas where caribou have easy access to open habitats in summer, these areas appear to be highly attractive to the animals. Simkin (1960) noted that woodland caribou in northern Ontario utilized beach ridges, windswept lakeshores, and open bogs in the summer, presumably to rid themselves of insects. Coniferous shoreline areas are also heavily used by woodland caribou (Stevens and Storey 1977). In mountainous areas, woodland caribou appear to take the opportunity to move into open, alpine areas during the summer (Edwards and Ritcey 1960; Stelfox et al. 1978).

3.1.1.4 Summer habitat use by woodland caribou in the AOSERP study area. The data which are available concerning the summer habitat use by woodland caribou in the AOSERP study area appear to be fairly similar to that reported by workers elsewhere in the boreal forest.

As during the winter, the majority of caribou relocations in the AOSERP study area were from lowland areas, particularly the black spruce-muskeg cover type (Fuller and Keith in prep. a). However, several other cover types appeared important.

Marked increased utilization of open muskeg areas occurred in May as new growth appeared (Fuller and Keith in prep. a). A slight increase in use of aspen, aspen-conifer, and conifer-burn cover types was noted during spring and summer, which Fuller and Keith (in prep. a) felt corresponded to increased abundance of vascular vegetation.

3.1.2 Seasonal Movements of Woodland Caribou

The majority of work which has been conducted concerning seasonal movements of caribou populations concerns the spectacular long-range migrations of large numbers of the barren-ground caribou. Until recently, relatively little work has been conducted concerning the boreal forest forms of caribou.

The concensus of available information suggests, however, that the woodland caribou tends to be more solitary than gregarious and that the seasonal movements of woodland caribou are restricted to relatively short shifts in range (Freddy and Erickson 1975; Stardom 1975; Shoesmith and Storey 1977; Fuller and Keith in prep. a).

Most past information available consists of observations of tracks or apparent shifts in population density and lacks any real quantification. Simkin (1965) stated that woodland caribou may well have once been migratory; however, such is not the case now. Simkin (1965) believed that herds in the southern and western portion of their range in Ontario were non-migratory, with each herd confined to relatively small islands of suitable habitat. In Manitoba, seasonal movements and migrations may be characteristic of specific herds; Guymer (1957) reported northward movements of woodland caribou in April in the Pas-Cranberry Portage area and to the southeast of Norway House, while Carbyn (1968) indicated seasonal shifts of caribou in the Bloodvein River area. Seasonal shifts in elevation have been reported for caribou occupying mountainous terrain (Edwards and Ritcey 1959; Stelfox et al. 1978).

Two studies which used radio-collared animals are available on the seasonal movements of woodland caribou (Shoesmith and Storey 1977; Fuller and Keith in prep. a). It was apparent in both studies that woodland caribou have no specific herd migrations, nor specific wintering, calving, summering, or rutting areas. Rather, individual animals appear to have traditional seasonal ranges and movements which appear to be independent of those of other caribou in the region. Traditional use of seasonal ranges from year to year was obvious in four adult females radio-collared by Shoesmith and Story (1977). Fuller and Keith (in prep. a) report on the movements of only one female; between March 1976 and December 1977 its activities were confined to an area of approximately 840 km^2 with no apparent seasonal range shifts. However, the movements which are reported for the five male woodland caribou all indicate that individuals made "traditional" spring and late fall movements between traditional wintering and summering grounds (Fuller and Keith in prep. a.: Figures 46 and 47). Additional movements were made during the rut by some bulls.

The area over which individual woodland caribou range does not appear to be large. Shoesmith and Storey (1977) show that the summer range of woodland caribou in Manitoba averaged 13 km^2; the full range of woodland caribou in Manitoba was 69.3 km^2. Fuller and Keith (in prep. a) report on the total area used by individual woodland caribou in the AOSERP study area, including all seasonal movements. They report that cows range over an average of 493 km^2 while bulls range over 1,007 km^2; the larger range for males was primarily due to their greater seasonal migrations.

Therefore, it appears that seasonal movements of woodland caribou are relatively small in extent and that movements are undertaken independently by individual animals rather than as a herd by the entire population.

3.2 SUSCEPTIBILITY OF WOODLAND CARIBOU TO DEVELOPMENT PROJECTS

As the susceptibility of both the ungulate species (woodland caribou and moose) on the AOSERP area are basically similar, discussion of the susceptibility of both species will be combined and will be presented in the section dealing with moose (4.2).

3.3 POPULATION DYNAMICS OF WOODLAND CARIBOU

Although the subspecies of caribou which occurs in the AOSERP study area is the woodland caribou, data from the other subspecies of wild caribou in continental Canada will be used, where appropriate, to supplement the data on population dynamics specific to this subspecies.

3.3.1 Population Density

The densities of various woodland caribou populations in Canada are presented in Table 1. Although the densities of woodland caribou show considerable variability, they are generally not high, except for populations in Labrador. In Labrador, population densities of up to 25.1 caribou/10 km^2 have been reported (Table 1); however, it is unclear whether these densities were based upon the total range of the herds or simply on the areas in which caribou were concentrated during the surveys. With the exception of Labrador, woodland caribou densities have rarely been reported to exceed 1.0/10 km^2 and generally range between 0.05 and 0.5 caribou/10 km^2 (Table 1).

3.3.1.1 Population densities of woodland caribou on the AOSERP study area. In the AOSERP study area, the population densities of woodland caribou in the Birch Mountains have been reported to be between 0.16 and 0.44/10 km^2 (Fuller and Keith in prep. a). This figure fits well within the range of densities reported for most other boreal forest areas (Table 1); however, despite the fact that caribou also occur in the southern portions of the AOSERP study area, no data are available for any area except the Birch Mountains.

Table 1. Population densities of woodland caribou in various areas of the boreal forest.

Location	Observed Density of Woodland Caribou (#/10 km^2)	Source
Mealy Mountain Labrador (Newfoundland)	0.79 - 3.9[a]	Bergerud (1967)
Muskrat Lake Labrador (Newfoundland)	16.9[a]	Bergerud (1963)
Paradise River Labrador (Newfoundland)	25.1[a]	Bergerud (1963)
Island of Newfoundland	0.49 - 0.69[a]	Bergerud (1971b)
Hudson Bay Lowland (Ontario)	0.50[a]	Simkin (1965)
Gods River - Pipestone River (Ontario)	present[a]	Fischer et al. (1977a)
Northwestern Ontario	0.03[a]	Simkin (1965)
Round Lake (Ontario)	0.03[a]	Addison (1971)
Western Ontario	0.11[a]	Simkin (1965)
Sandy Lake (Ontario)	0.04[a]	Simkin (1962a)
Attawapiskat - Wunnummin Area (Ontario)	0.08[a]	Goddard (1961)
Geraldton District (Ontario)	0.09[a]	Ontario Ministry Natural Resources (1958)

continued...

Table 1. Concluded.

Location	Observed Density of Woodland Caribou (#/10 km^2)	Source
Nakina (Ontario)	0.19[a]	Timmermann (1976)
Nelson River - Gods River (Manitoba)	0.46[a]	Fischer et al. (1977a)
Gods River Area (Manitoba)	0.39 - 1.2[a]	REDCC (undated)
Churchill River Area (Manitoba)	low[a]	Koonz and Storey (1975)
LaRonge West (Saskatchewan)	0.17[a]	Ruttan (1960)
Sled Lake (Saskatchewan)	1.37[b]	Ruttan (1960)
Jasper National Park (Alberta)	0.57[a, b]	Stelfox and Warden Service (1974)
Selkerk Mountains (British Columbia)	0.08[a, b]	Freddy (1974)
Fort Simpson (N.W.T.)	0.05[a]	Wooley and Wooley (1976)
AOSERP study area (Birch Mountains)	0.16 - 0.44[a]	Fuller and Keith (in prep. a, b)

[a] Based on aerial surveys.
[b] Based on ground studies.

Therefore, the distribution of woodland caribou throughout the AOSERP study area is not known; moreover, densities of woodland caribou in the Birch Mountains are suspected to be unrepresentative of those over the remainder of the study area (Fuller and Keith in prep. b).

3.3.1.2 Relationship between habitat quality and population density. The density which a wildlife population can achieve and maintain in a given area is ultimately governed by the limitations placed upon it by the environment, i.e., the carrying capacity of the habitat (Dasmann 1964). It has been shown that a large variation exists in the densities which woodland caribou populations are able to achieve in various locations within the boreal forest. Cringan (1957) has shown that the density of woodland caribou in an area is related to the proportion of suitable mature coniferous forest which exists in the area. Therefore, it appears that the habitat quality of an area determines the upper limit on the density of woodland caribou populations and is the factor which ultimately regulates population density. The proximate factors which act to regulate population densities of woodland caribou at or below the carrying capacity will be discussed later.

3.3.2 Population Structure

Population structure is determined by the numerical relationships between the sexes and ages within it (Dasmann 1964). The structure of a population, and its capacity to withstand and recover from losses, is determined by the balance of natality and mortality.

3.3.2.1 Natality rate. Natality is the major factor determining the potential yield from, and productivity of, a population. It is influenced by many factors including: sex ratio, litter size and frequency, and percentage of breeding females.

3.3.2.1.1 Sex ratio. Determination of range-wide sex ratios in caribou populations in highly difficult since sexual segregation may be recognized among barren-ground caribou at all seasons and young bulls of all caribou subspecies are very difficult to distinguish from antlerless adult cows (Kelsall 1968; Simkin 1965). The male:female ratios which have been observed for several woodland and barren-ground caribou populations are presented in Table 2. There is general agreement that females outnumber males; the typical adult male:female sex ratio in caribou populations appears to fluctuate around 1:2 (Kelsall 1968; Skoog 1968; Bergerud 1971b, 1974a).

3.3.2.1.2 Sex ratio of woodland caribou on the AOSERP study area. The sex ratio of woodland caribou on the AOSERP study area is 1:1.5 (Table 2). This appears to be slightly tipped in favour of males in comparison to other caribou populations in Canada.

3.3.2.1.3 Litter size and frequency. Caribou typically have only one young per year; however, twins have been occasionally reported (Banfield 1974; McEwan 1971). No data are available concerning the frequency of twinning in woodland caribou.

3.3.2.1.4 Percentage of breeding females. Female caribou do not usually reach breeding age until 28 months of age and frequently not until 40 months (Skoog 1968; Bergerud 1971b, 1974a). There is relatively little known about the percentage of females which breed within each age class; however, there appears to be a relatively close agreement in the overall pregnancy rates of female caribou from many different herds of several of the subspecies of caribou in North America (Table 3). It appears that, on the average, approximately 80 percent of the adult females in a caribou population will produce a calf each year. Further, there appears to be little variation in the pregnancy rate which can be attributed to variation in quality of range (Bergerud 1974a). There are no data available from the AOSERP study area concerning the percentage of female caribou which breed.

Table 2. Fall sex and age ratios of various caribou populations in Canada.

Area	Male:Female Ratio	% Adults	% Yearlings	% Calves	Population Status	Sources
Buchans Plateau[a] (Newfoundland)	1:2.35	74.3	6.4	19.2	Increasing	Bergerud (1971b)
Interior Herd[a] (Newfoundland)	1:2.62	76.4	10.3	13.4	Increasing	Bergerud (1971b)
Avalon Herd[a] (Newfoundland)	1:1.52	65.1	15.1	19.8	Increasing	Bergerud (1971b)
Gaspe (Quebec)[a]	-	-	-	16.0	Stable	Bergerud (1974a)
Attawapiskat-Wannummin (Ontario)[a]	-	81.0	NA	19.0	?	Goddard (1961)
Northwestern Ontario[a]	-	83.3	NA[c]	16.7	?	Simkin (1965)
Jasper National Park[a] (Alberta)	1:2.14	79.5	NA	20.5	?	Stelfox and Warden Service (1974)
Wells Gray[a] (British Columbia)	-	-	-	19.0	Increasing	Bergerud (1974a)
Selkirk Mountains[a] (British Columbia)	1:2.5	73.6	NA	26.4	?	Schroeder (1973)
Bluenose Herd[b]	-	-	-	14.1	Increasing	Thomas (1969)
Bathurst Herd[b]	-	-	-	12.3	Increasing	Thomas (1969)
"Western Ranges"[b]	-	-	-	15.9	?	Kelsall (1969)
Beverly Herd[b]	-	-	-	12.0	Increasing	Thomas (1969)
Kaminuriak Herd[b]	1:1.82	-	-	9.0	Decreasing	Parker (1972)
Porcupine Herd[b]	1:1.27	59.2	21.9	18.9	Stable	Jakimchuk et al (1974)
AOSERP Study Area[a]	1:1.5	83.6		16.4	?	Fuller and Keith (in prep. b)

[a] Woodland caribou.
[b] Barren-ground caribou.
[c] NA = category not applicable.

Table 3. The percentage of females which calved and proportion of calves in the population immediately after calving in several caribou populations.

AREA	% of Females which calved	% Calves of Total Population Immediately After Calving	Source
Interior Herd[a] (Newfoundland)	84.0	34.3	Bergerud (1971b)
Avalon Peninsula Herd[a] (Newfoundland)	74.5	26.7	Bergerud (1971b)
Irregular Lake[a] (Ontario)	86.1	35.2	Simkin (1965)
Kaminuriak Herd[b] (N.W.T.)	86.4	30.0	Dauphine (1976) and Parker (1972)
Beverly Herd[b] (N.W.T.)	78.0	-	McEwan (1963)
Nelchina Herd[b] (Alaska)	89.0	-	Skoog (1968)
Porcupine Herd[b] (Yukon)	-	23.7	Bente and Roseneau (1978)

[a] Woodland caribou.
[b] Barren-ground caribou.

3.3.2.1.5 Productivity. On the basis of the foregoing review, two generalities may be made:

1. The sex ratio of adults in most caribou populations in continental Canada approximates 1 male:2 females, regardless of subspecies, and
2. Approximately 80 percent of the adult females produce one calf in each year.

Therefore, at birth, calves should represent approximately 35 percent of the total population. It would appear that calves indeed do typically represent between 26 and 35 percent of the populations for which data are available (Table 3). No comparable data are available for the AOSERP study area.

3.3.2.2 Mortality rate. The factor which acts to counterbalance natality is mortality. If the natality rates and mortality rates are equal, the population size will remain stable. The mortality rate of caribou varies with age.

3.3.2.2.1 Mortality of calves--annual recruitment rate. The annual recruitment can be defined as the number of young animals which survive their first year of life. Bergerud (1971b) indicates that the mortality rate of calves aged 6 months old and older is identical to the mortality rate of adults; the mean percentage of calves in the Interior herd, Newfoundland, was not significantly different between October and April in the period 1956 to 1964. These data are in agreement with most other published information concerning the timing of mortality of caribou calves (Skoog 1968; Kelsall 1968; Parker 1972; Nowosad 1975). It is, therefore, common practice to express recruitment rate of caribou populations as the percentage of calves in the late fall and winter population (Thomas 1969; Bergerud 1971b).

Table 2 contains a summary of the fall age ratios which have been observed in various caribou populations in Canada. It appears that considerable variability exists in the recruitment rates which have been reported for caribou populations. Some of this variation likely results from errors in sampling; Parker

(1972) reports that at no time during his study were all sex and age classes represented in any one area in the ratio that actually existed within the population. Further variation appears to be due to the exposure of the population to predation; Bergerud (1971b) reported higher calf survival in areas which had lower predator densities. However, it appears that by autumn or winter, most caribou herds contain only about 15 percent calves. Therefore, it appears that an average of approximately 50 percent of the calves born during a given year will not survive the first six months (Bergerud 1971b, 1974a). Calf mortality can, however, be very much higher; Parker (1972) reports that calf survival in the Kaminuriak herd averaged only 22 percent during the period 1967-1969, while F. Miller (1974a) reports that virtually the entire calf crop of this herd was wiped out in 1962.

Fuller and Keith (in prep. a, c) report that calves make up 12 to 16.4 percent of the population on the AOSERP study area. This figure appears to be within the range shown by other caribou populations.

3.3.2.2.2 Mortality of adults. The mortality rate of adults includes mortality from hunting and predation. Bergerud (1971a) and Parker (1972) both consider hunting loss to be incremental to predation losses; therefore, the total annual loss of adults will vary with the level of hunting pressure to which the population is subjected. However, several estimates of the natural mortality rate of adults are available. Bergerud (1971a) has shown that the natural mortality of adult woodland caribou in Newfoundland was estimated at 6 percent for the Avalon Peninsula herd, and 5 percent for the Interior herd. Parker (1972) indicated that the mortality rate of adult caribou of the Kaminuriak herd was 4.3 percent; Parker felt that wolves were harvesting only that proportion of the population that would normally be lost to other mortality factors.

3.3.2.2.3 Mortality of adults on the AOSERP study area. Fuller and Keith (in prep. b) report that the mortality of radio-collared adult woodland caribou on the AOSERP study area was estimated to be 18 to 23 percent; two of their radio-collared adults were killed by wolves and three others died of unknown causes.

3.3.3 Population Regulation of Caribou

As noted previously, the quality of the habitat is the factor which sets the upper limit which populations will reach and which ultimately regulates population size. However, there is strong evidence that caribou populations never attain the densities which could theoretically be supported by the habitat (Bergerud 1974a). Walters et al. (*in* Bergerud 1974a) concluded that the caribou range in the eastern Canadian arctic could support a density of 5 caribou/km^2; the population estimate at that time was only 0.35 caribou/km^2. Kelsall (1968) reported a density of approximately 2.6 caribou/km^2 for Canadian mainland populations in the late 1950's. It is clear, therefore, that caribou populations are regulated by factors more proximate than the carrying capacity of the range.

Two major studies of population regulation are available for Canadian caribou herds: Bergerud (1971b), who studied woodland caribou in Newfoundland, and Parker (1972) and Miller and Broughton (1974), who studied barren-ground caribou in the eastern arctic. All authors agree that mortality resulting from predation and hunting are the factors which currently act to control population growth.

3.3.3.1 Wolf predation. In pristine situations caribou populations are thought to have maintained a fine balance between recruitment and mortality, with predation being the most limiting and consistent mortality factor (Bergerud 1971b; Walters et al. (*in* Bergerud 1974a). As noted earlier, the reproductive rate of caribou is relatively low, yet they are hunted by an extremely effective predator--wolf. Bergerud (1971a) has stated that the wolf appears to have the characteristics necessary to allow it to regulate caribou numbers. The footloadings of both wolves and caribou in snow are similar and both species avoid deep soft snows (Nasimovich 1955). The wolf is highly mobile and, therefore, should be able to search out caribou in most habitats and at all seasons, with the possible exception of spring, when a portion of the wolf population is limited in travel by the need to care for pups. Thus, it appears that caribou populations have no refugia from their major predator; the presence of prey refugia probably accounts for a great many of the balanced predator-prey systems that exist in nature (Wilson and Bossert 1971). Errington (1946, 1956, 1967) felt that canid predation on ungulates was an exception to his generalization that predators took mostly surplus animals and did not act to limit numbers.

Bergerud (1971b) documented the average annual mortality rate of adult woodland caribou from natural causes, including predation, was between 5 and 6 percent. Both Parker (1972) and Miller and Broughton (1974) have shown that wolves selectively kill caribou calves, as opposed to adults, on both the summer and winter ranges. Parker (1972) concludes that wolves are harvesting only that proportion of adult caribou which would have been normally lost to natural mortality factors. Therefore, wolf predation on adult caribou does not appear to be a critical factor limiting caribou populations.

As noted, approximately 50 percent of all caribou calves die prior to reaching 6 months of age. A large number of potential causes exist for such high calf mortality, such as birth defects, disease, chilling, and predation. Kelsall (1968) felt that the chilling of neonatal calves was the most important mortality factor; however, his data showed that calf survival increased when wolves were poisoned. Moreover, it appears that, as the availability of calves to predators would be positively correlated with the number that survived post-natal mortality due to weather, a form of compensating mortality would exist since the availability of calves to predators in summer and winter would be negatively correlated to June mortality (Bergerud 1974a). Bergerud (1971b) compared calf survival data from his Pot Hill study area, where predators were not removed, and his Middle Ridge study area, where predators had been removed. Calf survival in June 1965 at Pot Hill was only 49 percent as compared to 35 percent at Middle Ridge; in June the following year (1966) only 4.7 percent of the calves remained at Pot Hill while 27.5 percent remained at Middle Ridge. The effects of predator removal were still evident two years later (June 1967) when only 2.9 percent of the 1965 calves remained at Pot Hill as compared to 10.2 percent at Middle Ridge. Therefore, it appears that the calves which were removed by predators were not "surplus" to the population (*sensu* Errington 1946, 1956, 1967) and would not have died from other causes in the absence of predation; therefore, predators did, in fact, act to reduce the rate of increase in the caribou population.

Further evidence that wolves may be able to regulate caribou populations is available from barren-ground caribou studies. Parker (1972) has shown that the Kaminuriak herd had an average annual recruitment rate of between 9 and 10 percent during the three years of his study (1966-1969). This annual recruitment was in close balance with annual mortality of adults, estimated at 10.0 percent. Parker (1972) believed that winter predation on caribou by wolves was the main contributing factor in the high loss of calves. Parker (1972) concluded that it was possible that wolf predation, in combination with the level of harvest occurring during his study, might control the Kaminuriak herd.

Elsewhere in North America, there is evidence that wolves may have been able to limit the growth of the Valchina herd, Alaska (Skoog 1968; Bergerud 1971b).

3.3.3.2 Hunting mortality. As noted above, most authors consider that, because of their high natural mortality rate and low reproductive rate, caribou populations are in fine balance between gains and losses; hunting mortality is sufficient to upset this balance and cause declines in caribou populations.

There is evidence from several herds to indicate that hunting losses were sufficient to control or reduce population numbers. Bergerud (1971a) has calculated that, due to the naturally low recruitment rate of caribou, hunting mortality was probably the cause of the decline of caribou herds in Newfoundland from 40,000 to 2,000 between 1915 and 1930. Illegal hunting appeared to be an important check on growth of the Northern Peninsula and Humber River, Newfoundland, herds during the period 1957 to 1967 (Bergerud 1971a). Bergerud (1971a) considers that the law of diminishing hunting returns, which generally applies to hunted populations, is an ineffective check on exploitation of caribou populations. This is especially true where caribou are a primary source of fresh meat, such as was the case in Newfoundland in the early 1900's and is currently the case with many native settlements throughout Canada and Alaska. Parker (1972) has shown that native hunters killed approximately 5.3 percent of the Kaminuriak herd during 1967-68; given the natural mortality rate of 4.8 percent and the recruitment rate of only 10 percent, Parker (1972) concludes that this level of hunting mortality, in combination with natural mortality, was sufficient to prevent the herd from increasing in numbers. In the succeeding eight year period (1968-69 to 1975-76), the native harvest of caribou from this herd has increased over three-fold from the 2,363 reported by Parker (1972) to approximately 7,100 in 1975-76 (Fischer et al. 1977b). The increased level of harvest appears to be, at least in part, responsible for the substantial decline in this herd noted during the last several years (Fischer et al. 1977b; Thompson et al. 1978). Overhunting, in combination with high natural mortality losses due to wolf predation, was generally held to be responsible for the spectacular decline in the Arctic herd in Alaska.

Calef (1978) reports that two of the nine herds of barren-ground caribou in the Northwest Territories are currently decreasing; the hunting mortality of these two herds is 8.8 percent and 12.4 percent of the population. The Bathurst herd has 4.4 percent of the population killed by hunters but appears stable while the other six herds, which have between 0 and 1.8 percent of the population killed each year by hunters, are either stable or increasing (Calef 1978).

It seems clear, therefore, that the high natural mortality rate of calves due to wolf predation is the main factor controlling caribou populations and generally maintains a close balance between gains and losses; this balance may be easily upset by unregulated hunting by natives or by illegal hunting.

4. MOOSE

4.1 SEASONAL POPULATION DISPERSION

Two major topics must be discussed to gain a knowledge of the seasonal population dispersion of moose: seasonal distribution in relation to habitat and seasonal movements.

4.1.1 Seasonal Distribution in Relation to Habitat

4.1.1.1 Winter habitat use. Winter habitat use by moose is governed by the need for food and is affected by snow depths (Fischer et al. 1977a).

It has been well established that moose are primarily a browsing species, especially during winter (Peek 1974). Table 4 presents a summary of the major winter food species of moose in boreal North America. It is evident on the basis of this summary that the species which are preferred as winter food by moose are characteristic of successional rather than climax vegetation associations; similar conclusions have been drawn by other workers who have reviewed moose habits (Peterson 1953; Kelsall and Telfer 1974; Peek 1974; Fischer et al. 1977a).

Data which are available concerning the winter diet of moose in the AOSERP study area indicate that no major variation exists between the food preferences of moose in the AOSERP study area and the winter food preferences of moose elsewhere in the boreal forest (Nowlin in prep.).

Habitat selection by moose may be correlated with the availability of palatable browse (Pimlott 1961; Kelsall and Telfer 1974; Peek et al. 1976). Thus, important moose habitats in the boreal forest are typically those produced during early stages of plant succession (Peterson 1953; Krefting 1974). Two major types of seral habitats exist within the boreal forest: those permanently, but dynamically, in a seral stage due to a continuing disturbance (riparian areas), and those temporarily in a seral stage due to a single episode of disturbance (burns, logged areas, etc.). The general characteristics of moose winter habitat in North America are summarized in Table 5.

Table 4. Major winter foods of moose in North America.

Location	Major Food Species	Source
Mt. McKinley Park, Alaska	Willows (*Salix* spp.), Dwarf birch (*Betula nana*), aspen (*Populus* spp.)	Murie (1944)
South-central Alaska	Willows (*Salix* spp.), birch (*Betula* spp.), aspen (*Populus tremuloides*), cottonwood (*Populus balsamifera*)	Spencer and Chatelain (1953)
Keni Peninsula, Alaska	Willows (*Salix* spp.), bog birch (*Betula glandulosa*), Dwarf birch (*Betula nana*), Saskatoon (*Amelanchier alnifolia*), mountain ash (*Sorbus scopulina*), high-bush cranberry (*Viburnum edule*)	Spencer and Hakala (1964)
Cypress Hills, Alberta	Saskatoon (*Amelchanier alnifolia*), aspen poplar (*Populus tremuloides*), chokecherry (*Prunus virginiana*), pin cherry (*Prunus pennsylvanica*)	Barrett (1972)
Northern Alberta	Saskatoon (*Amelchanier alnifolia*), willow (*Salix planifolia, Salix bebbiana, Salix myrtillifolia, Salix serissima*), birch (*Betula* spp.), high-bush cranberry (*Viburnum edule*)	Nowlin (in prep.)
East-central Saskatchewan	Aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), willow (*Salix* spp.), chokecherry (*Prunus virginiana*), red-osier dogwood (*Cornus stolonifera*) Saskatoon (*Amelanchier alnifolia*)	Stewart et al. (1977)
Northern Manitoba	Red-osier dogwood (*Cornus stolonifera*), willows (*Salix* spp.), aspen (*Populus tremuloides*), cranberry (*Viburnum* spp.), box elder (*Acer negundo*), balsam poplar (*Populus balsamifera*)	Peek (1974)
Ontario	Balsam fir (*Abies balsamea*), willow (*Salix* spp.), white birch (*Betula papyrifera*), beaked Hazel (*Corylus cornuta*), aspen (*Populus tremuloides*), pin cherry (*Prunus pennsylvanica*)	Peterson (1953)
Laurentide Park, Quebec	Balsam fir (*Abies balsamea*), mountain maple (*Acer spicatum*), white birch (*Betula papyrifera*), willows (*Salix* spp.), red-osier dogwood (*Cornus stolinifera*), pin cherry (*Prunus pennsylvanica*)	DesMeules (1965)
Nova Scotia	Yellow birch (*Betula alleghanensis*), speckled alder (*Alnus rugosa*), honeysuckle (*Lonicera* spp.), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), mountain maple (*Acer spicatum*), blackberry (*Rubus* spp.)	Telfer (1967)
Newfoundland	Balsam fir (*Albies balsamea*), white birch (*Betula apyrifera*), raspberry (*Rubus* spp.), pin cherry (*Prunus pennsylvanica*), aspen (*Populus tremuloides*), yew (*Taxus canadensis*)	Dodds (1960), Pimlott (1953), Bergerud and Manuel (1968)

continued...

Table 4. Concluded.

Location	Major Food Species	Source
Isle Royale, Michigan	White birch (*Betula papyrifera*), aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), willows (*Salix* spp.), mountain ash (*Sorbus americana*), red-osier dogwood (*Cornus stolinifera*)	Aldous and Krefting (1946) Krefting (1951)
North-eastern Minnesota	Willows (*Salix* spp.), aspen (*Populus tremuloides*), white birch (*Betula paparifera*), beaked Hazel (*Corylus cornuta*), pin cherry (*Prunus pennsylvanica*)	Peek (1971)

Table 5. Characteristics of winter moose habitat in various areas of North America.

Location	Habitat Characteristics	Source
Alaska	Riparian seral communities, post burn seral communities, willows are key browse species.	LeResche et al. (1974)
Susitna River, Alaska	Riparian and subalpine willow communities, old burns and glacial outwash areas are prime winter habitats.	LeResche et al. (1974)
South central Alaska	Disturbed areas with willow-birch growth or aspen regeneration.	Spencer and Chatelaine (1953)
Northern Yukon and Mackenzie Valley	Riparian zones along rivers and streams, old burns.	Watson et al. (1973)
Northwestern Alberta	Willow flats or deciduous-mixedwood stands with suitable browse species.	Pendergast et al. (1974)
Fort McMurray area, Alberta	Alder and willow communities occurring on wet sites.	Penner (1976)
Fort McMurray area, Alberta	Aspen stands heavily used for feeding and bedding.	Nowlin (in prep.)
Northern Saskatchewan and Manitoba; southern district of Mackenzie	Heaviest use occurred in 1 to 50 year old burns.	Scotter (1967)
Northeastern Manitoba; Northwestern Ontario	Riparian shrublands, closed coniferous forests, and mixed-woods were the most heavily used habitats.	Fischer et al. (1977a)
West-central Manitoba	Burns, gently sloping till plains interspersed with organic deposits; wet areas with willow-alder stands, and aspen balsam poplar and birch dominated uplands supported the highest moose densities.	Hildebrand and Jacobson (1974)
Quebec	Sites disturbed by fire, logging or insects, deciduous-boreal forest ecotones and southern exposures with moderate slopes support the greatest numbers.	Brassard et al. (1974)
New Brunswick	Open deciduous and coniferous stands (old burns); dense coniferous stands may be important in late winter.	Telfer (1970)
Nova Scotia	Extensively clearcut forests dominated by softwoods and heavy shrub growth.	Telfer (1967)
Newfoundland	Spruce-balsam fir forest interspersed with burns, clearcuts, lakes and shrub barrens.	Bergerud and Manual (1969)

continued...

Table 5. Concluded.

Location	Habitat Characteristics	Source
Northeastern Minnesota	Extensively burned lowlands supporting a mixture of aspen, spruce, white birch, balsam fir and jackpine in various age classes.	Van Ballenberghe and Peek (1971)
Northwestern Minnesota	Prairie-mixedwood ecotone with marsh, willow stands, hardwoods and abandoned fields in different stages of succession.	Phillips et al. (1973)
Montana-Wyoming	Riparian communities dominated by willows mixed with alders, red-osier dogwood and silver berry; conifer stands are used for bedding and escape.	Peek (1974)
Jackson Hole, Wyoming	Cottonwood and willow growth along river valleys.	Harry (1957)

Frequent flooding and ice-scouring act to maintain the seral vegetation of riparian areas. Willows (*Salix* spp.), alder (*Alnus rugosa*), dogwood (*Cornus stolonifera*), aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) characterize riparian habitats in Alberta and typify the riparian zone throughout the boreal forest (Raup 1935; Moss 1955). Watson et al. (1973) state that riparian areas provide the majority of the most critical winter moose habitat in the Mackenzie Valley and northern Yukon. They further state that, in winter, these critical habitats may support the population from a surrounding area which is 5 to 10 times as large as the wintering area itself. Wooley and Wooley (1976) show that moose in the Fort Simpson, N.W.T. area make considerable use of river valley habitats during winter. In the Norman Wells area, riparian willow stands are also heavily utilized by moose during winter (Wooley et al. 1976; Wooley and Wooley 1976; Walton-Rankin 1975). LeResche et al. (1974) state that the seral riparian communities are the key winter ranges in much of Alaska. Moose in northwestern Alberta have been shown to heavily utilize valley and riparian habitats, particularly in willow flats or other areas where red-osier dogwood, sapling poplar, and other suitable browse species were present (Pendergast et al. 1974). Penner (1976) showed that moose in the Fort McMurray, Alberta, area showed a distinct preference for tall shrub habitats in wet areas. Harry (1957) and Houston (1968) reported that floodplain vegetation provides the majority of moose winter range near Jackson Hole, Wyoming, with densities ranging up to 19.5 moose/km^2. Willow bottoms are also the most extensively used winter range near Ruby River, Montana (Knowlton 1960). Berg and Phillips (1974) reported that willow and associated willow habitats in alluvial areas of northwestern Minnesota are much more heavily used than non-willow habitats.

Fires and other disturbances have a contributing role in creation of the seral vegetation required by moose (Hatter 1950; Peterson 1953; Watson et al. 1973; Krefting 1974; Kelsall and Telfer 1974). Throughout the boreal forest, disturbances such as burning typically result in rapid regeneration to deciduous browse species such as willows, alders, birch, dogwood, and aspen (Moss 1955; Rowe 1959). Seral burn habitats become extremely important winter habitat once growth of the regenerating shrubs is sufficient to provide available browse above the winter snow level (LeResche et al. 1974). Spencer and Chatelain (1953) estimated that the Kenai burn, Alaska, took three years before regeneration was sufficient to produce significant quantities of moose browse. LeResche et al. (1974) suggest that the value of burns in Alaska as winter moose habitat is greatest from 20 to 25 years after the burn, then slowly declines with the abundance of deciduous browse species as the community matures and complete coniferous cover returns. The "useful life" of most burns appears to be about 50 years (LeResche et al. 1974); however, this is variable depending upon site characteristics. Scotter (1964) noted that, in boreal black spruce and white birch forests of Saskatchewan, 121 moose pellet groups per ha were present in 1 to 10 year old regeneration but only 22.2 per ha were present in forests over 120 years old. Scotter (1964) also concluded that moose prefer habitat which is less than 50 years old. Modification of the range by fire was found to be the most important factor in determining moose distribution and abundance in northern Manitoba (Bryant 1955). Krefting (1974) indicated that fire has been responsible for producing the assortment of high quality seral-stage moose habitats on Isle Royale. Thus, it is generally concluded that fires or other temporary disturbances result in a marked, if temporary, improvement of moose habitat in temperate and boreal North America (Leopold and Darling 1953a, 1953b; Pimlott 1953, 1961; Peterson 1955; Scotter 1964; Cumming 1972; Dodds 1974; Fischer et al. 1977a). Indeed, Krefting (1974) recommended the use of prescribed burning or cutting as a method of producing moose habitat.

In winter, movements of moose are hindered and habitat selection is influenced by depth and quality of snow (Telfer 1967; Kelsall 1969; Peek 1971; Peek et al. 1976). Telfer (1967) felt that snow deeper than 90 cm seriously hindered moose movement. Nasimovitch (1955) noted that moose movements were unaffected by snow depths of 40 to 50 cm, while movement was definitely impeded by depths of 60 to 70 cm. Kelsall (1969) reported that moose movements were unrestricted by 44 cm of snow but severely restricted by depths of over 70 cm. Coady (1974) concludes that snow depths of up to 40 cm cause little or no hindrance of moose movements, from 40 to 60 cm movement is only slightly restricted, at depths of 70 cm movement is definitely impeded, while at depths greater than 90 cm movement is restricted sufficiently that adequate food intake may become impossible. Both Nasimovitch (1955) and Kelsall and Telfer (1974) believe that moose probably cannot survive in areas where soft snow greater than 70 cm is of common and long-lasting occurrence. However, moose appear to be able to occupy some areas of deep snow by taking advantage of the lesser snow depths which occur under the tree canopies (Kelsall and Telfer 1974).

As winter advances and snow accumulates, moose typically move from the open, seral communities into the more dense cover which is generally found in the more mature forest stands (DesMeules 1965; Chamberlin 1972; Telfer 1970; Kelsall and Prescott 1971; Peek 1971; Van Ballenberge and Peek 1971; Coady 1974). Uncrusted snow over 90 cm deep resulted in a high use of coniferous cover by moose in New Brunswick (Telfer 1970); further, the tendency for moose to travel on shallower snow under forest cover appeared to increase with snow depth (Kelsall and Prescott 1971). Peek (1971) reported that moose shifted to dense cover when snow depths were only 45 cm or less. Dense coniferous areas may be important to moose as bedding and escape cover. During mid-winter, moose beds are most common in the densest cover (Peek et al. 1976). Similarly, Stone (1971) reported the use of coniferous forests as moose bedding cover. Knowlton (1960) suggested that coniferous forests are used as escape cover. Both Mech (1970) and Peterson (1955) suggest that dense cover is used by moose as escape terrain. Thus, it is well documented that moose inhabit areas where snow depth allows bedding in comfort and unimpeded movement to feeding areas (Dodds 1974).

The influence of snow depths on habitat use by moose in the AOSERP study area may not be important, as snow depths in northern Alberta do not generally reach the level where they become critical to moose (Kelsall and Telfer 1974).

4.1.1.2 Winter habitat use by moose in the AOSERP study area. The habitat selection patterns of moose in the AOSERP study area appear to be similar to those reported elsewhere in the boreal forest (Nowlin in prep.). Penner (1976) shows that during late winter moose exhibited a preference for tall shrub habitats and an avoidance of coniferous cover types.

4.1.1.3 Summer habitat use. Summer habitat use by moose appears to depend, at least in part, on the summer food habits. Studies of the summer food habits of moose suggest that they eat a greater proportion of forbs, graminoids, and aquatics during the summer than during the winter; however, browse continues to constitute the bulk of the diet. Table 6 summarizes information concerning the summer food habits of moose in various areas of North America. No specific data are available concerning the summer diet of moose in the AOSERP study area; however, it is unlikely that any major variation exists between the summer food preferences of moose in the AOSERP study area and the summer food preferences of moose elsewhere in the boreal forest.

Information on summer habitat use by moose is relatively poor. However, several major points appear consistently. Moose appear to make extensive use of aquatic habitats during summer, where these habitats are available. Hosley (1949) termed moose "semi-aquatic" during the summer. Peterson (1955) suggests that, during summer, moose make considerable use of marsh areas in Ontario. Van Ballenberghe and Peek (1971) report that in northeastern Minnesota moose make considerable use of aquatic feeding sites during the summer. Heavy use of aquatics was also reported from British Columbia (Ritcey and Verbeek 1969), Ontario (de Vos

Table 6. Major summer foods of moose in North America.

Location	Major Food Species	Source
Kenai Peninsula, Alaska	Birch (*Betula* spp.), cloudberry (*Rubus chamaemorus*), sundew (*Drosera rotundifolia*), fireweed (*Epilobium* spp.), lupine (*Lupinus* spp.), mushrooms (*Boletus* spp.), sedges (*Carex* spp.), horsetails (*Equisetum* spp.), grasses, aquatic vegetation	LeResche and Davis (1973)
Mount McKinley Park, Alaska	Willows (*Salix* spp.), Dwarf birch (*Betula glandulosa*), Aspen (*Populus tremuloides*), sedges (*Carex* spp., *Eriophorum* spp.), various grasses, various herbs, and submerged vegetation	Murie (1944)
Bowron Lake Park, British Columbia	Primarily aquatic vegetation (*Equisetum* spp., *Sparganium* spp., *Potomageton* spp.)	Ritcey and Verbeek (1969)
Newfoundland	Primarily grasses, sedges and leaves of deciduous shrubs, few aquatics taken	Dodds (1960)
Isle Royale	Mountain maple (*Acer spicatum*), balsam fir (*Abies balsamea*), aspen (*Populus tremuloides*)	Krefting (1951)
Isle Royale	Aspen (*Populus tremuloides*), alder (*Alnus* spp.), pin cherry (*Prunus pennsylvanica*), yew honeysuckle (*Lonicera* spp.), mountain maple (*Acer spicatum*), raspberry (*Rubus* spp.), willow (*Salix* spp.), sedge (*Carex* spp.), grasses, mushrooms, horsetails (*Equisetum* spp.), aster (*Aster* spp.), pondweeds (*Potomageton* spp.), wood fern (*Dryopteris* spp.). marsh marigold (*Galtha palustris*), jewel weed (*Impatiens* spp.), and pond lilies (*Nymphaea* spp., *Castalia* spp.)	Murie (1934)
Northern Minnesota	Willows (*Salix* spp.), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), pin cherry (*Prunus pennsylvanica*), mountain maple (*Acer spicatum*), mountain ash (*Sorbus* spp.), Red-osier dogwood (*Cornus stolonifera*), yellow pond lily (*Nuphar variegatum*), wild rice (*Zizania aquatica*), burreed (*Sparganium* spp.), calla (*Calla palustris*), and pondweed (*Potomageton* spp.)	Peek (1971, 1974)

...continued

Table 6. Concluded.

Location	Major Food Species	Source
Yellowstone National Park	Willows (*Salix* spp.), aquatic vegetation, grasses and forbs	McMillan (1953)
Gravelly Mountains, Montana	Willows (*Salix* spp.), current and gooseberry (*Ribes* spp.), aspen (*Populus tremuloides*), snowberry (*Symphoricarpos albus*), buffalo-berry (*Shepherdia canadensis*), sticky geranium (*Geranium viscossissimum*), lupine (*Lupinus* spp.), cinquefoil (*Potentilla gracilis*), larkspur (*Delphinium* spp.), umbrella plant (*Eriogonum* spp.), and sorrel (*Rumex* spp.)	Knowlton (1960)
Jackson Hole, Wyoming	Willow (*Salix* spp.), aspen (*Populus tremuloides*), menziesia (*Menziesia ferruginea*), thimbleberry (*Rubus parviflorus*), honeysuckle (*Lonicera* spp.), fireweed (*Epilobium* spp.), water crowfoot (*Runuculus aquatilis*), and pondweed (*Potomageton* spp.)	Houston (1968)

1958), and Wyoming (Denniston 1956). In the Tanana Flats, Alaska, moose commonly feed in herbaceous bogs from spring thaw to late summer; greatest use of this habitat appears to be during early to mid-summer (LeResche et al. 1974).

Riparian and tall willow habitats continue to be heavily used in summer. Le Resche et al. (1974) consider riparian willow communities to be year-round habitats for moose; during late summer moose in Alaska frequently feed in tall shrub communities. During summer, 78 percent of moose observed in the Peace-Athabasca Delta, Alberta were in marsh and open willow habitats (Berg and Phillips 1974); similarly, moose in the Saskatchewan River delta frequent willow areas or willow edges. Phillips et al. (1973) reported moose in northwestern Minnesota showed a marked increase in the use of low and open willow types in spring. Van Ballenberghe and Peek (1971) suggest that moose may spend considerable time in lowlands adjacent to water. Peek (1971) often noted moose in stands adjacent to waterways which provided aquatic plants.

As summer progresses, moose appear to make increasing use of upland deciduous habitats. Kearney and Gilbert (1976) show that while tall shrub habitats continued to be important, moose showed an increased use of the upland deciduous stands during July and August. Peek et al. (1976) note that upland habitats dominated by aspen and white birch, which were moderately stocked and relatively mature, received the major share of use by moose during the summer; they suggest that shifts in habitat use as summer progresses may be correlated with decreased palatability of open grown and aquatic species which mature more quickly, and therefore become less succulent, than plants growing beneath shade.

4.1.1.4 Summer habitat use by moose in the AOSERP study area. No specific data are available concerning the summer habitat use by moose in the AOSERP study area; however, it is unlikely that summer habitat use by moose in the AOSERP study area shows any major variation from summer habitat use by moose elsewhere in the boreal forest.

4.1.2 Seasonal Movements of Moose

Moose populations in North America vary from the extremes of sedentary to truly migratory, with every degree of migrating behaviour in between being represented. LeResche (1974) has reviewed the movement patterns of moose populations in North America. Movement between separate seasonal home ranges (i.e., winter range to summer range) provides the impetus for seasonal movements. All seasonal movement patterns reported for moose represent one of three general types: Type A, short-distance movements between two seasonal ranges with little change in elevation; Type B, medium- to long-distance movements between seasonal home ranges with significant differences in elevation between high summer-fall ranges and lower winter ranges; and Type C, medium- to long-distance movements between three distinct seasonal ranges with significant differences in elevation between high summer-fall ranges and lower winter and spring ranges (LeResche 1974). Movements are made by individual moose rather than by the population or portions of the population. Migrations of individuals follow traditional routes, although the timing may vary annually, based upon environmental factors. Regular moose migrations of between 1 and 179 km have been reported; the shortest migrations occur in flat areas with little environmental gradient.

Movements of individual moose in the AOSERP study area have been reported by Hauge et al. (in prep.). Four of the 7 radio-collared bulls and 2 of the 15 radio-collared cows made movements of between 36 and 55 km between summer and winter range; the remaining animals were, apparently, sedentary. It would appear that movements of moose in the AOSERP study area are generally of LeResche's (1974) type A; however, not all moose make movements. The AOSERP study area generally exhibits little environmental or altitudinal gradient.

4.2 POTENTIAL IMPACTS OF LARGE DEVELOPMENT PROJECTS ON MOOSE

Since the susceptibility of moose to large development projects is basically similar to that of woodland caribou and other ungulates, the susceptibility of ungulates in general to large development projects will be considered.

Any major development project in the AOSERP study area will undoubtedly interact with ungulates. The effects of such interactions on individuals will determine the ultimate impact of the development project on the population. Therefore, it is critical to determine the types of interactions which will occur and the effects of those interactions on individuals in the population.

Previous to 1970, wildlife biologists placed little emphasis on research dealing with the effects of human activities on ungulate populations. However, increasing public concern over the effects of northern pipeline construction in Canada and Alaska, as well as the realization of the probable effects of other development projects, intensified interest in the field. To date, however, much of the data accumulated on this subject lacks quantification. In addition, most studies have dealt primarily with the barren-ground caribou and elk; few data are available concerning the effect of large development projects on other ungulates such as moose and woodland caribou. Therefore, in reviewing the literature on the effects of large development projects on ungulates, we have drawn heavily upon data concerning barren-ground caribou and have supplemented these data with other specific information, where such information is available.

Any major development project on the AOSERP study area will result in two main types of interactions between ungulates and the project: direct interactions will occur through the effects of sensory disturbances and through the agents of direct mortality; and indirect interactions between ungulates and the project will result through the alteration of habitat. Examples of these types of interactions, and their effects, have been reported in the scientific literature.

4.2.1 Sensory Disturbances

Sensory disturbances may result from the noise and activities associated with any development project. Such disturbances may cause varying levels of stress which are typically expressed as altered behaviour and, hence, altered, and usually increased, energy requirements.

Individuals which are already experiencing relatively high energy requirements due to either environmental factors (i.e., cold) and/or the particular period in their life cycle (i.e., pregnancy) are the most vulnerable to additional energy requirements. Sensory disturbances at such critical times can cause changes in the energy budget of individuals in the population which can result in significant reductions in natality or increases in mortality or both.

Detrimental effects of sensory disturbance vary from direct mortality including desertion or trampling of calves during herd stampedes (Klein 1973; Urquhart 1973; Geist 1975; Surrendi and DeBock 1975); injury or death of individuals stumbling or falling (Urquhart 1973; Gray 1972); abortion of foetuses in pregnant cows as a result of long chases or striking of the abdomen on snow crusts or in falls, or displacement of foetuses, causing complications at birth (Geist 1971). Dispersal of herds may result in increased predation by wolves (Gray 1972; Geist 1975). Animals may damage their lungs or have increased susceptibility to disease after running in cold weather (Geist 1971; 1975).

More subtle physiological responses also occur, which may have a number of effects. Geist (1975) reported that the energy expenditure of animals increased by 25 percent during chronic excitation, while lower levels of activity caused an 8-fold increase and high levels of activity may increase this to 20-fold. At certain times of year (winter and during periods of insect harassment) ungulates may be at a food intake level between basal and maintenance requirements. Studies of domestic reindeer (a species closely related to caribou) have shown that these animals also experience heavy demands on their energy resources during the fly season (Zhigunov 1961) and during the rutting season (Thomson 1971; Lent 1964). As energy conversion of food to work is only 20-25 percent, the animal may quickly be put into a negative energy balance. Use of fat reserves lowers chances of animal survival, particularly if the animal is initially in poor condition (Geist 1975; Gray 1972; Klein 1973). Geist (1971) calculated the raised cost of living as 1.0-1.4 kcal $kg^{0.73}$/d during mild excitation, while walking cost

2.4 kcal kg$^{0.73}$/h and running 60 kcal kg$^{0.73}$/h. Amount of energy used is a function of the intensity and duration of excitation and the distance and elevations covered as well as the decrease in food intake (Geist 1975). This increased requirement is at the expense of fat storage, body and antler growth, or reproduction. Other physiological results of stress include metabolic changes, abnormal sexual behaviour, resorption of embryos after 17 percent loss of body weight, and reduced fertility. Critical seasons include late pregnancy and calving, extremely cold weather, or periods of insect harassment when the animals are also in poor condition due to loss of blood and reduced food intake (Geist 1971, 1975; Urquhart 1973; Klein 1973).

Other results of sensory disturbances to ungulates are avoidance or abandonment of ranges, leading to a loss of access to resources, increased predation, or increased cost of existence (Geist 1975).

Caribou have been described by some investigators as naturally curious and frequently unwary (Lent 1964; Kelsall 1968). They do, however, react with fright and/or flight responses to a number of disturbing stimuli, such as potential predators and scavengers (wolves, Golden Eagle, red fox, grizzly bear, gulls); humans (hunters, hikers); and machines (helicopters, fixed-wing aircraft, and snowmobiles) (Lent 1964; Klein 1971; Thomson 1973; Riewe 1973). There is evidence that caribou and reindeer react to human disturbance, whether on foot, snowmobile, or aircraft, with the same types of basic fright and escape reactions that they demonstrate toward natural predators and scavengers (Lent 1964; Kelsall 1968; Gaare et al. 1970; Thomson 1973; McCourt et al. 1974b). Despite a certain degree of unwariness, caribou can be disturbed by man's activities and presence. Lent (1964) discusses an interesting observation of the response of caribou to "inuksuit" ("likeness of man"). These piles of stone 0.3-0.6 m high were apparently used to herd caribou and reindeer. People stationed at intervals along the lines of "inuksuit" reinforced the caribou's reaction to them with noise and motion. Whether caribou would react to "inuksuit" without being conditoned to do so is unknown.

Schultz and Bailey (1978) showed that humans approaching elk off roads caused elk to leave open areas. Ward (1976) has shown that elk preferred to be at least 0.8 km from people engaged in forestry operations. Stelfox and Bindernagel (1978) report that the sight and/or smell of humans caused woodland caribou to interrupt grazing at distances up to 700 m; however, interruption of grazing usually occurred at distances less than 350 m. Woodland caribou were observed to take flight from humans at distances of 700 m;, however, flight reactions typically occurred at distances less than 200 m (Stelfox and Bindernagel 1978). Many other studies also suggest that human activity will affect the behaviour, distribution, and habitat use of ungulates (Walther 1969; Dauphine and McClure 1974; Batcheler 1968; Moran 1973; Ward 1973; Rost 1975).

Aircraft overflights are generally considered disturbing to ungulates. The effect of aircraft on caribou decreases with increasing distance (Fischer et al. 1977b). It is believed that aircraft are most disturbing to wildlife during take-off and landing manoeuvers; thus, the most significant interactions will be expected to occur near landing facilities. Studies of barren-ground caribou have shown that caribou infrequently show strong reactions to light fixed-wing aircraft flying higher than 180 m above ground level (Klein 1973; Calef and Lortie 1973; McCourt et al. 1974b; McCourt and Horstman 1974; Surrendi and DeBock 1976; Fischer et al. 1977b).

The group size, presence or absence of calves within a group, phenological season, orientation, type of aircraft, prior exposure to aircraft, and prior activity of the caribou also affect the strength of the response of caribou to overflying aircraft (Fischer et al. 1977b). Caribou in large groups appear to be most responsive to aircraft disturbance (Klein 1973; McCourt and Horstman 1974; Fischer et al. 1977b); they are most responsive during late winter, calving and post-calving periods (McCourt and Horstman 1974; Calef et al. 1976; Fischer et al. 1977b). Reaction of ungulates is generally greater to helicopters than to fixed-wing aircraft (Klein 1973; Surrendi and DeBock 1976). Surrendi and DeBock (1976) indicated that caribou sensitivity to disturbance increased in wooded habitat.

Moose in the Yukon Territory and Alaska showed less reaction to aircraft than did caribou (Klein 1973; McCourt et al. 1974b). The same authors found that grizzly bears showed the greatest sensitivity to aircraft, often running when the aircraft was still distant.

Ungulate disturbance caused by other forms of mobile equipment (snowmobiles, vehicles) is likely affected by factors similar to those influencing aircraft disturbance. Roby (1978) showed that the activity budgets of caribou groups greater than 300 m from the Trans-Alaska pipeline haul road were not significantly different from the activity of undisturbed caribou. Surrendi and DeBock (1976) noted that barren-ground caribou approached the Dempster Highway cautiously and caribou movements were often interrupted or deflected. Slow-moving vehicles caused caribou to avoid the road, while fast-moving vehicles produced a panic reaction and a retreat of up to 16 km from the road. Bergerud (1974c) stated that caribou might not cross a road upon which they continuously perceived moving vehicles. Perry and Overly (1976) found that roads reduce big game use of adjacent habitat located from road edge to more than 0.8 km (0.5 mi) away. Hershey and Leege (1976) indicated that elk avoided using areas within 0.4 km (0.25 mi) of roads and showed a strong preference for areas further than 0.4 km from a road. Even very low levels of snowmobile activity have been shown to result in displacement of deer (Dorrace et al. 1975; Baldwin and Stoddard 1973). Bergerud (1971b) concluded that the motion of trains was the major factor which caused woodland caribou to avoid railways.

Observations of the reactions of ungulates to stationary machinery suggest that noise is the major factor influencing response (Kelsall 1968; Bergerud 1974c). McCourt et al. (1974b) reported that barren-ground caribou avoided an area within 0.2 km of a simulated compressor station. Slaney (1975) and Gray (1972) reported that caribou and muskoxen did not react noticeably to seismic shots at a distance of 3 km to 6 km. In Newfoundland, Bergerud (1974c) observed no visible reaction of caribou to the sound of dynamite and suggested that noise disturbances in the absence of sight or scent usually have little impact. Bergerud (1974c) claimed that for woodland caribou which were habituated to highway traffic, car noise constituted only a temporary alert; the sound of railroad trains, in the absence of visual stimuli, had little effect on woodland caribou. Espmark (1972) observed the reactions of a small herd of domestic reindeer to sonic booms and found that their behaviour was not seriously affected, regardless of boom intensity. However, he also stated that Laplanders avoid keeping large herds in corrals during thunderstorms because large congregations of reindeer may display serious panic reactions to sudden and intense disturbances. Mytton and Keith (in prep.) conclude that their data concerning the effects of gas well disturbance on moose were insufficient to permit meaningful analysis.

Cover is likely an important factor influencing the intensity of sensory disturbance of terrestrial mammals. Availability of cover and, therefore, intensity of disturbance is also a factor of animal size; in any situation, small animals can make better use of available cover and, consequently, should be more immune to the effects of sensory disturbance than large animals.

4.2.2 Agents of direct mortality

Direct physical harm causing death of or injury to animals may result from collisions with vehicles, accidents, such as entanglement with wire, contact with or ingestion of environmental contaminants, or from the recreational activities of employees of a development project. Direct mortality of ungulates may also result from accidents, primarily collisions with vehicles. Klein (1971) reported that road traffic kills considerable numbers of reindeer in northern Europe; in Finland, reported losses of reindeer through highway accidents were 1,252, 1,262, and 1,474 during 1967, 1968, and 1969, respectively. Road kills were, however, relatively infrequent during construction of the Alyeska pipeline (K. Morehouse, U.S. Fish and Wildlife Service, Anchorage, Alaska, pers. comm.). R. Flanagen (Superintendent Jasper National Park, Jasper, Alberta, letter dated 10 April 1978) reported that 186 elk, moose, sheep, and deer were killed by vehicles and trains in Jasper National Park between 1973 and 1975. Grenier (1973) reports that road kills accounted for between 15 and 20 percent of the exploitation of moose populations living near the roads in Laurentides Park, Quebec; there was a positive correlation between numbers of vehicles and number of moose killed.

It appears that the impacts which highways and similar corridors will have on ungulate populations are a function of the location of the facility relative to habitat and the construction and maintenance procedures. Grenier (1973) has shown that the distribution of ecological requirements, such as ponds, were important factors determining the impact of roads on moose populations. Similarly the relationship between deer activity and deer-automobile collisions have been shown to be functions of highway location relative to deer requisites such as feeding and resting areas and to the relative availability of feeding areas other than the highway right-of-way (Carbaugh et al. 1975; Reilly and Green 1974; Bellis and Graves 1971). Ungulates appear to be attracted to road rights-of-way by the highly palatable forage typically used to revegetate banks and by the availability of salt due to de-icing procedures (Stelfox 1972; Grenier 1973). Raush (1956) documented the attraction for moose of the cleared rail line rights-of-way in Alaska and the subsequent mortality suffered by these populations.

It is generally considered that the completion of a major development project, such as a pipeline, will result in changes in recreational and subsistence land uses resulting in an alteration of the traditional resource harvesting pattern of the area (Polar Gas 1977).

Caribou are extremely vulnerable to hunting; caribou live in the open, have traditional, predictable movements, do not perceive danger at great distances and, under continual harassment, do not appear to become more wary towards man (Bergerud 1974a). Bergerud (1974a) has concluded that the decline in caribou numbers in North America following settlement was due to increased human hunting coupled with increased natural predation. Skoog (1968) and Lent (1966) have suggested that the total disappearance of the caribou from the Seward Peninsula-Lower Yukon in the 19th century may have been due to heavy human activity. Bergerud (1967) stated that overhunting resulted in a decline in Labrador caribou.

The attraction of people to work on major development projects, and the increased access provided by the development and construction of ancillary facilities, such as roads through previously inaccessable regions, combine to produce increased hunting pressure on ungulates. Leege (1976) related the decline of the Peteking, Idaho, elk herd to overharvest by hunters which resulted from increased access provided to a previously isolated area due to newly constructed logging roads. Oregon has recently instituted controls on vehicle access to certain areas for the purposes of hunting (Coggins 1976).

Most development projects will result in toxic materials entering the environment from four major sources: (1) exhaust emissions of equipment, which will contain carbon monoxide (CO), nitgrogen oxides (NO_x), sulphur oxides (SO_x) and various particulates; (2) industrial chemicals used in construction and operation, which will include various chlorinated hydrocarbons (pesticides and herbicides), polychlorinated biphenyls (plastics, resins, neoprene, etc.) and freezing point depressants (menthos); and (3) accidents, which will include spills of fuels and lubricants, and the possible venting of sour gas ($_2$S); and (4) camps which will produce human wastes and garbage dumps.

Five factors interact to determine the impact of a particular toxic substance on mammals: the amount introduced, the frequency of release, the areal extent of release, the persistence of the material, and the toxicity of the material.

Exhaust emissions are unlikely to ever reach the level where they are directly harmful. However, the sensitivitity of lichens to sulphur dioxide is well known; in the presence of sulphur dioxide, lichens show reduced growth rates or death (Hale 1967). Therefore, a long-term effect of air pollution may be the reduction in lichens throughout the affected area. Any significant reduction of lichens in wintering areas of caribou will result in a corresponding reduction in the range carrying capacity.

Chemicals containing chlorinated hydrocarbons and polychlorinated biphenyls (PCB's) are often used in industrial projects. These materials are very resistant to degradation and persist in the environment over long periods of time. Additionally, both are capable of undergoing biological magnification (Hunt and Bischoff 1960; Jensen et al. 1969). The effects of these materials may, therefore, be widespread and long-term. There is evidence that sublethal concentrations of chlorinated hydrocarbons may impare mammalian reproduction (Klein 1972), perhaps as a result of steroid imbalance (Clarke 1972). Other sublethal effects of PCB's on mammals include a wide variety of pathologic changes in various organs (Peakall and Lincer 1970).

Accidental spills will result in fuels and lubricants being introduced into the environment. Mammals may ingest oil by eating oil-covered food or licking their fur. Ingestion of oil may result in adenomatous lesions of the colon (Lushbaugh and Hackett 1948), hyperkeratosis (Sikes et al. 1952), and hyperplastic changes in stomach mucosa (Sunderland et al. 1951). However, spills of oil products are likely to be small in volume and, despite the persistence and toxicity of oil products, are unlikely to produce major effects on mammal populations.

4.2.3 Habitat alteration

An industrial project can have significant effects on wildlife should it alter, destroy, or otherwise remove a significant proportion of an important wildlife habitat. The loss of any seasonally essential component of the year-round range is as critical to a population as loss of its entire range. An important habitat that is uncommon or rare is by virtue of its rarity more vulnerable to significant alteration or loss than is a common or widespread habitat. Habitat alterations will affect animals directly by loss of habitat through destruction or vegetation alteration and indirectly by the avoidance of areas due to disturbance.

In the AOSERP study area, developments will result in long-term habitat loss because vegetation will be removed from large areas for long periods of time and will be slow to regenerate. The direct loss of ungulates which may be expected to result from any development project due to destruction of habitat may be estimated from a knowledge of the amount of each type of habitat lost to the project and the seasonal importance of each habitat type to ungulates.

Revegetation occurring subsequent to any development will replace any habitat which was lost. Moose populations will, however, respond to revegetated areas much more quickly than will caribou. Kelsall et al. (1977) consider that the optimium successional stages for moose occur between 11 and 30 years after burning. Stelfox et al. (1973) report that moose will avoid large logged areas for at least 15 years, or until the regenerating forest provides adequate cover. Woodland caribou, on the other hand, appear to prefer the mature forests. Cringan (1956) noted that moose decline and woodland caribou increase as the boreal forest matures. Stelfox and Taber (1969) reached a similar conclusion for the coniferous forests of the northern Rocky Mountains.

Another significant source of habitat loss is likely to result from ungulate avoidance of areas during the period of construction and operation of major developments. Although the area which will be avoided by ungulates because of various disturbances is poorly known, avoidance of small distances from either side of a linear development could result in the loss of significant amounts of habitat. McCourt et al. (1974b) reported that barren-ground caribou avoided an area within 0.2 km of a simulated compressor station. Ward (1976) has shown that elk prefer to remain at least 0.8 km from forestry operations.

The alteration of the vegetational characteristics of an area may also occur as a result of industrial developments. The emission of even trace amounts of sulphur dioxide may result in a decreased productivity of lichens and, hence, a decreased productivity of caribou (Hale 1967). Herbicides applied along rights-of-way have been shown to create early seral conditions (Bramble and Byrnes 1972, 1974); such conditions might have positive impacts on moose populations but would have negative impacts on caribou populations.

Areas subject to major developments may also face increased risk of fire.

Construction of pipelines, roads, seismic lines, buildings, etc. would constitute a structural change in the environment. Because of the plasticity of ungulate responses to structural components of the environment, one might expect that they would likely adapt to this change fairly readily, assuming the facility did not constitute an impassable barrier. Animals encounter natural barriers in the form of rivers and gorges during their movements. Although these often result in some deflection, they do not interfere significantly with movements between different parts of the range. Bergerud (1974c) observed that caribou adapted readily to simple structural changes such as roads and railroads. Movements of vehicles, however, caused temporary alert behaviour, presumably because of the phylogenically based response to moving objects established during a long history of caribou-wolf interactions. Bergerud's observations are corroborated by those of Klein (1971) in Scandinavia. He noted that highways and railroads have obstructed movements of wild reindeer.

There is evidence that ungulates may be affected somewhat by linear physical disturbance of the landscape. For example, Klein (1971) observed that hydroelectric projects have had a severely disruptive effect on reindeer movements because of the absolute barrier which the large impoundments often impose. Fences are also absolute barriers and are used extensively in Scandinavia to simplify reindeer herding procedures and in North America to restrict ungulate access to roadways (Reed et al. 1974; Puglisi et al. 1974). Child (1973) indicates that the majority of caribou which approached his pipeline simulations showed a tendency to avoid the structures, and either paralleled the simulations to their terminals or reversed their direction of movement. Roby (1978) has shown that disturbed caribou, particularly cows with calves, avoided the Trans-Alaska pipeline corridor. Cameron and Whitten (1977) suggest that, as a result of avoidance of the Trans-Alaska pipeline corridor, the Central Arctic herd is undergoing a separation into two components, each located on opposite sides of the corridor. High snowbanks may also hamper caribou movements; snowbanks higher than 1.5 m prevented caribou from crossing ploughed roads (Urquhart 1973; Surrendi and DeBock 1976). Caribou in Alaska tended to select the points of lowest elevation for crossing the haul road along the Trans-Alaska pipeline (Cameron and Whitten 1976).

However, there is also evidence that habituation to linear terrain disturbances may take place quickly. Child (1973) observed that the crossing success of caribou groups that repeatedly encountered the pipelines throughout the summer was significantly correlated with the number of occasions when animals were present at the simulations. Urquhart (1973) reported that, in winter, caribou deflected for some distance by new seismic lines whereas they crossed older lines without hesitation. White et al. (1975) found that a resident caribou herd on the North Slope habituated to road traffic. Roby (1978) reports that bull caribou may be able to adapt to elevated sections of pipeline.

Skrobov (1972) reported on observations of the response of wild reindeer on the Taimyr Peninsula, U.S.S.R. to highways, railroads, and above-ground water and gas pipelines. Skrobov's observations of the reaction of reindeer to roads and railways are similar to those of Bergerud (1974c) and Klein (1971). The animals crossed roads and railways most readily when traffic was not heavy. The water pipeline was also crossed. After the gas pipeline was completed, reindeer on spring migration often moved parallel to the line until they found a place blown over with snow or where the ravines were deep enough so that they could pass under the pipeline. During the following migrations, the reindeer circumvented the pipeline. No information on the design of the pipeline was included in Skrobov's report; however, Klein (1974) reports that the pipe is on wood pilings which raise it 30 to 50 cm above the ground surface, although where it passes over depressions, ravines, etc., clearance may be two or more metres). Klein (1974) states that 2 m is the minimum clearance which allows passage by reindeer.

In some cases, even almost absolute barriers are overcome by caribou which are motivated by a strong traditional behavioral pattern in the presence of the more plastic response to structural components of the environment. Observations by Miller et al. (1972) of the response of migrating caribou to a corral illustrate the secondary importance of a relatively significant structural modification in the presence of traditional migratory behaviour. Caribou either overcame or circumvented the barrier and continued on their set course.

It is apparent from this review that very little data has been accumulated concerning the effects of large developments specifically on woodland caribou and moose; however, the data which are available specifically for woodland caribou and moose appear to suggest that the reactions of these ungulates are approximately the same order as those of other ungulates.

4.3 POPULATION DYNAMICS OF MOOSE

4.3.1 Population Density

In Canada, moose commonly range throughout the boreal forest and, occasionally, into the forest-tundra transition or even tundra areas (Kelsall 1972). The densities of moose which have been reported for a variety of locations throughout Canada are presented in Table 7. It is clear that considerable variation exists in the densities of moose at various locations in Canada.

Table 7. The density of various moose populations in Canada.

Location	Moose Density Moose/km^2	Source
Northeastern Alberta, Oil Sands Development Area	0.31	Department of Environment (1973)
Syncrude Lease 17 - near Fort McMurray, Alberta	0.23 - 0.27	Penner (1976)
AOSERP Study Area, near Fort McMurray, Alberta	0.19	Cook and Jacobson (in prep.)
Fort McMurray - mineable of the bituminous sand area	0.27 - 0.31	Bibaud (1973), Bibaud and Archer (1973)
Big Game Zone 1, Northern Alberta	0.23	Phillips and Pattison (1972)
Swan Hills, Alberta	0.62 - 1.12	Lynch (1973)
Edson Region, Alberta	0.62 - 0.66	Lynch (1973)
Peace River, Alberta	0.58 - 1.5	Stelfox (1962)
Peace River, British Columbia	0.96	Penner (1976)
Clear Hills, Alberta	0.50	Hall et al. (1973)
Wapitiarea, Alberta	1.08	Hall et al. (1973)
Rochester, Alberta	1.62	Frokjer and Keith (in prep.)
Clear River, Alberta	0.69 - 2.33	Stelfox (1962)

continued...

Table 7. Concluded.

Location	Moose Density Moose/km^2	Source
Saskatchewan River Delta (Cumberland House)	0.46 - 0.58	Churchill River Study (1976)
North Central Saskatchewan and Manitoba	0.02 - 0.22	Churchill River Study (1976)
Northern Manitoba	0.003	Fischer et al. (1977a)
Big Trout Lake, Ontario	0.006	Simkin (1962a)
Sandy Lake - Sachigo Lake, Ontario	0.03	Simkin (1962b)
Hudson Bay Lowlands, Ontario	0.002	Simkin (1961)
Lake Nipigon, Ontario	0.06 - 0.11	Timmermann (1975, 1976)
Fort Simpson, N.W.T.	0.00 - 0.02	Wooley and Wooley (1976)

4.3.1.1 Population density of moose on the AOSERP study area. Little variation appears to exist between the moose population densities which have been reported for various areas of the AOSERP study area (Table 7); extreme values ranged only from 0.19 moose/km^2 (Cook and Jacobson in prep.) to 0.31 moose/km^2 (Dept. of Environment 1974; Biband 1973; Biband and Archer 1973).

4.3.1.2 Relationship between habitat quality and population density. As noted, moose population densities show considerable site-to-site variation within the boreal forest. There would appear to be a consensus that the local abundance of moose varies with the successional stages of the forest areas (Kelsall et al. 1977). Mature coniferous forests are able to support few moose; however, successional growth, which contains abundant browse, is able to support high moose densities. Geist (1971) suggests that, since moose habitat is relatively lacking in permanence, moose have evolved the behavioural characteristics which allow them to rapidly colonize areas of newly created habitat. Peek (1974) documented an example of a widely dispersed, low density moose population which rapidly colonized habitat which was created by fire. Peek (1974) showed that by 2 years after the fire moose densities had increased by six-fold on the burned area while the surrounding unburned area showed no increase in moose density.

Moose were also observed to rapidly colonize a large burn in south central Alaska, and the moose population was observed to rapidly increase on the burned area; moose densities were recorded as being 0.23/km^2, 0.29/km^2, 0.53/km^2, and 0.96/km^2 3, 4, 5, and 6 years, respectively after the fire (Spencer and Chatelain 1953; Peterson 1955).

Moose populations experience slow decline as seral vegetation matures (Geist 1971). Scotter (1964, 1970) has shown that the density of moose progressively declines from 31 to 120 years after fire with relatively little use being made of the mature forests. Krefting (1975) considers that fire is the most important factor influencing moose distribution presently and for at least several hundred years previously.

It appears, therefore, that moose population densities are highly variable both in time and in space, and that the moose density which exists in a given location at a given time will be largely dependent upon the quality of the habitat (Kelsall and Telfer 1974).

4.3.2 Sex Ratio

The male:female ratios which have been reported for a variety of moose populations are listed in Table 8. There would appear to be relatively wide variation in the sex ratios which are observed in various moose populations. However, several factors may account for the high variation which is observed in the sex ratio of moose populations. The relative visibility of various sex and age classes appears to be slightly different due to slightly different cover preferences (Frokjer and Keith in prep.). It is often not possible to distinguish males from females during aerial surveys; therefore, sex ratios which are based upon observational data are usually biased to cows (Simkin 1974). Hunting has a marked effect on the sex ratios of moose. Penner (1976) noted that a bias existed for the survival of bull moose in the AOSERP study area due to the "either-sex" hunting season and the subsistence harvest of moose in the Fort McMurray area. Analogous population trends are reported by Lynch (1973) in north-central Alberta and Finegan (1973) in southern British Columbia, where an increase in the proportion of bulls in the moose population occurred after antlerless moose hunting seasons were introduced. Bishop and Rausch (1974) report that the proportion of males in the Matanvska Valley, Alaska, was depressed due to "male only" hunting regulations. Simkin (1974) reports that the sex ratio of moose at 6 months of age is 1:1 and that, other than hunting, there is no known mortality factor which affects one sex more than another. Therefore, the sex ratios in a given population should be 1:1, unless some form of sex-differential mortality, such as hunting, has upset this ratio.

4.3.2.1 Sex ratio of moose on the AOSERP study area. The male to female sex ratio of moose on the AOSERP study area changed from 1:2.8 to 1:2.0 between January 1976 and January 1977 and to 1:1.4

Table 8. Composition of fall moose populations in various areas of North America.

		COMPOSITION OF FALL POPULATION				
Location	Male:Female Ratio	% Adults	% Yearlings	% Calves	Population Status	Source
North-central Alberta	1:2.7	74	NA[a]	26	-	Lynch (1973)
Peace River, British Columbia	1:2.4	52	NA	48	-	Penner (1976)
Wandering River/ Calling Lake, Alberta	1:3.7	82	NA	18	-	Hall et al. (1973)
Clear Hills, Alberta	1:4.8	84	NA	16	-	Hall et al. (1973)
Rochester, Alberta	1:2.4	44	16	40	Increasing	Frokjer and Keith (in prep.)
Elk Island Park, Alberta	1:1	61	18	21	Increasing	Blood (1966)
Ontario	1:1	57	18	25	Stable	Simkin (1974)
Quetico Provincial Park, Ontario	1:1.36	73	NA	27	-	Timmerman (1976)
Newfoundland	1:0.9	60	18	22	Stable	Pimlott (1959)
Newfoundland	-	NA	NA	22.9-29.4	-	Mercer (1974)
British Columbia	1:1	60	18	22	Stable	Edwards and Ritcey (1958)
British Columbia	1:2.2	78	NA	22	-	Finegan (1973)
Tanana Flats, Alaska (1960)	1:1.2	59	21.2	19.8	Increasing	Bishop and Rausch (1974)
Tanana Flats, Alaska (1966)	1:2.3	81.1	4.0	14.9	Decreasing	Bishop and Rausch (1974)
Nelchina Basin, Alaska (1953)	1:0.9	46.4	24.8	28.8	Increasing	Bishop and Rausch (1974)
Nelchina Basin, Alaska (1963)	1:1.8	65.4	14.0	20.6	Stable	Bishop and Rasuch (1974)
Nelchina Basin, Alaska (1972)	1:5.7	81.6	5.4	13.0	Decreasing	Bishop and Rausch (1974)
Northeastern Minnesota (1969)	1:1.3	73.0	8.0[b]	19.0	Decreasing	Peek et al. (1976)
Northeastern Minnesota (1970)	1:1.0	69.0	12.0[b]	19.0	Decreasing	Peek et al. (1976)
AOSERP Study Area						
Syncrude Lease #17	1:1.3	68	NA	32	-	Penner (1976)
Bitumount Study Area (1976)	-	71	NA	29	-	Hauge et al. (in prep.)
Bitumount Study Area (1977)	-	81	NA	19	-	Hauge et al. (in prep.)
Syncrude Study Area (1976)	-	70	NA	30	-	Hauge et al. (in prep.)
Syncrude Study Area (1977)	-	81	NA	19	-	Hauge et al. (in prep.)

[a] NA = category not used.

[b] Estimated based on double the proportion of yearling males.

in December 1977 (Hauge et al. in prep.); the bias which exists for bull survival on the AOSERP study area due to hunting has been discussed above.

4.3.3 Litter Size and Frequency

Moose only produce one litter per year; however, twinning is fairly common. Geist (1974) considers that the reproductive potential of moose has evolved primarily as a function of the rapidly expanding but slowly contracting habitats which moose colonize after forest fires remove climax forests and these are replaced by a deciduous flora favourable to moose. Selection for high reproductive rates in expanding populations of moose would favour the evolution of twinning; however, in areas with stable habitats, selection will favour the bearing of only a single calf (Geist 1974). Therefore, the twinning rate in moose populations appears to be highly variable; this variability has been attributed to the local range conditions (Pimlott 1959; Frokjer and Keith in prep.). For example, the twinning rate in the Caribou Mountain portion of the AOSERP study area was recorded as 44 percent, while in the Fort Hills portion of the study area the twinning rate was only 22 percent (Hauge et al. in prep.).

4.3.4 Percentage of Females Breeding

The percentage of females breeding shows variation with age. In reviewing the North American and Swedish literature on reproduction in moose, Simkin (1974) concludes that yearling moose will generally produce calves at a rate of 20 calves/100 cows while adult cows will produce at the rate of 113 calves/100 cows. Simkin (1974) notes that the pregnancy rate for adult moose shows relatively high consistency between populations but that the pregnancy rate for yearlings is more variable. Mytton and Keith (in prep.) report that 60 percent of all adult cow moose had calves near Rochester, Alberta.

4.3.5 Age Structure of the Population

The age structure of moose populations shows great variability depending upon the status of the population (Table 8); increasing populations are characterized by relatively high proportions of calves and yearlings while decreasing populations contain relatively larger proportions of adults. Simkin (1974) has concluded that a stable moose population will generally contain approximately 57 percent adults, 18 percent yearlings, and 25 percent calves; this ratio appears to be well in line with the age ratios seen in most stable moose populations (Table 8).

4.3.5.1 Age structure of the moose population on the AOSERP study area. The age distribution of moose on the AOSERP study area in mid-winter of 1975-76 appeared to signify a declining population; only about 9 percent of the population (excluding calves) was comprised of yearlings and 2 year olds (Hauge et al. in prep.). However, a significant increase in recruitment to the yearling cohart in 1977 markedly altered the population structure such that in mid-winter 1976-77 yearlings and 2 year olds comprised 39 percent of the population (Hauge et al. in prep.).

4.3.6 Productivity

Simkin (1974) has reviewed the data concerning productivity of moose populations in North America and has found them to be relatively similar, ranging between 31 and 36 percent; based upon a stable population containing 57 percent adult: 18 percent yearlings: 25 percent calves and a production of 20 calves/100 yearling cows and 119 calves/100 adult cows, Simkin calculates a calf production of 35 calves/100 moose. Increasing populations on good range will generally be more productive; Frokjer and Keith (in prep.) report that a rapidly expanding moose population near Rochester, Alberta has 40 percent calves.

4.3.7 Mortality Rate

The factor which acts to counterbalance natality is mortality. If the natality rates and mortality rates are equal, the population size will remain stable. The mortality rate of moose varies with age.

4.3.7.1 Mortality of calves and yearlings--annual recruitment rate. Two measures are commonly used as indices of the recruitment of young into moose populations: occurrence of calves in the fall population and the occurrence of yearlings in the fall population. The mortality rate for calves is highly variable and, as will be discussed later, appears to be a major factor influencing moose population levels. Rausch and Bratlie (1965) report that calf mortality for the first 11 to 13 months following parturition was 57 to 81 percent in 2 areas of Alaska. Peek et al. (1976) report that the estimated mortality of calves born on their study area during 1967 was 24 percent, while the mortality rate of the 1968 cohort was 61 percent. A "normal" mortality rate of 3-50 percent with mortality sometimes up to 80 percent has been reported for some areas in the U.S.S.R. (Heptner and Nasimowitsch 1967).

Some indication of the mortality rate of calves may also be obtained by comparing the relative proportion of calves and yearlings. In Simkin's (1974) stable population (57% adults: 18% yearlings: 25% calves) the mortality rate of calves would be estimated as 28 percent. Peterson (1955), in reviewing calf mortality in a large number of populations, concluded that the average calf mortality rate was about 29 percent.

Since the majority of the natural mortality in moose populations is borne by calves and yearlings (Peek et al. 1976) and since the minimum breeding age in moose is 2 years (Banfield 1974), the most commonly used statistic of recruitment ratio into moose populations is the occurrence of yearlings in the population (Pimlott 1959; Simkin 1974). Peterson (1955) concluded that the average annual recruitment of yearling moose usually falls between 12 and 25 percent and probably averages 15 to 17 percent. It is evident that decreasing populations have yearling percentages which are generally below 12 percent (Table 8).

Therefore, it appears that mortality rates of young moose, particularly calves, is the factor which generally acts to determine population levels (Gasaway et al. 1977).

4.3.7.2 Recruitment of calves and yearlings on the AOSERP study area. The mortality rate of moose calves on the AOSERP study area has shown considerable variability; 29 percent of the 1976-born calves died during their first 6 months as compared to 42 percent of the 1977-born calves (Hauge et al. in prep.). The proportion of calves in the fall population has shown similar variation; in 1976, calves made up between 29 percent and 30 percent of the population, while in 1977, calves accounted for only 19 percent of the population. The recruitment of yearlings appears to also show variability; during the winter of 1975-76, yearlings comprised only 9 percent of the population (excluding calves) while during the winter of 1976-77, yearlings made up 39 percent of the population (excluding calves) (Hauge et al. in prep.).

4.3.7.3 Mortality of yearling and adult moose on the AOSERP study area. Hauge et al. (in prep.) calculated the average mortality among 39 moose (yearlings and adults) of both sexes between 29 January and 31 December 1976 to be 17 percent; mortality averaged 27 percent among 43 moose between 1 January and 18 December 1977.

4.3.8 Population Regulation of Moose

There would appear to be a consensus that the local abundance of moose varies with the successional stages of the forest areas (Peterson 1955; Geist 1971; Kelsall and Telfer 1974; Kelsall et al. 1977); moose population density, therefore, appears to be ultimately dependent upon the quality of the habitat. However, several proximate factors are commonly cited as controlling growth rates of moose populations. In general, these proximate factors appear to act to depress the survival of calves and yearlings.

4.3.8.1 Winter weather. Winter weather, in particular snow depths, have often been implicated in reductions of moose populations.

Edwards (1956), who reported on ungulate abundance and weather records in British Columbia from 1900 to 1950, and Bishop and Rausch (1974), who reviewed the fluctuations of moose population levels in Alaska between 1950 and 1972, have all reached similar conclusions regarding the effects of snow conditions and moose populations. They conclude that deep snow conditions cause declines in ungulate abundance, that years of deep snow occur in groups rather than randomly, and that range conditions can modify the effect of snow conditions. MacLennan (1974) has shown that a large loss of calf and, perhaps, yearling moose occurred in both hunted and unhunted populations in Saskatchewan during the winter of 1971-72. Snow depth indices showed that the winter of 1971-72 had deep snow conditions comparable to only two other winters; in at least one of the two other winters with similar snow conditions, evidence indicated that die-offs of moose had also occurred. Following a period of increase, a substantial decline in moose numbers on the Tanana Flats, Alaska was precipitated by extreme snow severity in the winter of 1965-66, when as many as 50 percent of the population may have died (Bishop and Rausch 1974); survival of young moose was particularly low with reduced proportions of both calves and yearlings being evident in the 1966 population data. Production and survival of the Tanana population subsequently increased progressively through 1969. Declines in both survival and numbers of moose again occurred during 1970-71 in response to deep snow conditions (Bishop and Rausch 1974); in 1972, production and survival were again increased. The moose populations on the northern Kenai Peninsula showed a sharp decline in 1972 and 1973, when calves were essentially eliminated by greater than normal snow depths in the winters of 1971-72 and 1972-73; the mortality of older age classes was little affected (Bishop and Rausch 1974).

In all populations which were reviewed by Bishop and Rausch (1974), winter mortality due to snow depth was selective for calves.

Snow depths have the greatest effect on the mortality of the younger age classes both because calf moose have leg lengths which are approximately 10 to 15 percent less than adults (Kelsall and

Telfer 1974) and, therefore, cannot cope with deep snow as well as adults, and because calves have the lowest winter fat reserves of any segment of the population (MacLennen 1974).

The effects of snow depths appear to become relatively greater as habitat quality decreases; relatively small increases in snow depth were sufficient to cause extensive losses of calf moose in populations on qualitatively marginal range (Bishop and Rausch 1974).

4.3.8.2 Predation. Predation by wolves has been suspected to be one of the more influential factors regulating moose populations (Gasaway et al. 1977). Fuller and Keith (in prep. b) calculated that wolves accounted for 65 percent of the yearling and adult mortality annually in the Muskeg River drainage. Wolves were found to be controlling the moose populations of Isle Royale National Park (Mech 1966). Isle Royale supports at least 600 moose in late winter and produces an annual calf crop of 225, of which 85 survive their first year; the island also supports approximately 23 wolves, whick kill an average 140 calves and 83 adults per year (Mech 1970). Since the annual production of the moose herd and the annual kill by wolves are identical, wolves are taking enough moose to control the herd. Gasaway et al. (1977) reported that following the severe winter of 1970-71, moose numbers in the Tanana Valley and, consequently, total calf production reached a critically low point at which wolf predation limited calf survival and recruitment to levels which no longer sustained the moose population; the ratio of wolves to moose in the Tanana Valley was approximately 1:15 with a ratio of 1:43 for ungulates (includes sheep and caribou). Reduction of the ratio of wolves to moose to approximately 1:30 increased calf survival to that observed during previous years, when the population had been increasing (Gasaway et al. 1977). Mech (1970), in reviewing cases of control and non-control of ungulate populations by wolves, notes that definite control by wolves has been observed at prey-predator ratios of 3,352 kg (7,400 lb), 6,795 kg (15,000 lb) to 10,193 kg (22,500 lb), and 10,872 kg (24,000 lb) of prey per wolf; that two-thirds control by wolves is reported at a predator-prey ratio of approximately 10,419 kg (23,000 lb) of prey per wolf, and that little or no controlling influence is reported at ratios of 11,325 kg (25,000 lb) to 22,650 kg (50,000 lb), 23,728 kg (52,500 lb) and 40,770 kg (90,000 lb) to 120,000 kg (54,360 lb) of prey per wolf. Mech's (1970) conclusion was that wolf predation is the major controlling mortality factor where prey-predator ratios are 10,872 kg (24,000 lb) of prey per wolf or less, but that at higher ratios wolf predation cannot keep up with annual reproduction; it then becomes only one of several other contributing mortality factors and cannot be considered a primary controlling influence.

4.3.8.3 Other factors. The parasite *Parelaphostrongylus tenuis* has evolved a stable relationship with deer of the genus *Odocoileus* but causes heavy mortality in moose (Anderson 1972; Kelsall and Telfer 1974). Dense populations of white-tailed deer in parts of the deciduous-coniferous transition zone occupied by moose have lead to outbreaks of neurologic disease in moose which is caused by *P. tenuis* (Anderson 1972). Outbreaks of this parasite may be a limiting factor for moose, particularly in the southern and eastern portion of their range (Kelsall and Telfer 1974). At present the furthest west distribution of this is in southwestern Manitoba or southeastern Saskatchewan and does not therefore appear to occur in Alberta moose (J. Holmes pers. comm., Professor of Zoology, University of Alberta); however, there has been speculation that this parasite is moving westward.

5. WOLVES

5.1 SEASONAL POPULATION DISPERSION

Most wolves (*Canis lupus*) occur in packs. Those wolves that are solitary rarely comprise as much as 20 percent of the population and generally are socially and spatially isolated from packs (Mech 1970). Packs, therefore, are the units of population distribution that must be treated when examining the dispersion of wolves. During the breeding period, the wolf pack becomes centred around pup-rearing areas and, consequently, there is a seasonal change in the nature and pattern of its movements, as well as habitat use, from those of winter.

Wolves which prey in packs upon non-migratory prey usually establish territories (Mech 1970). As with many other Canidae, the wolf has evolved a complex system of social behaviour which ensures the maintenance of the pack as a hunting and breeding unit within a wolf population (Rabb et al. 1962; Rabb et al. 1967; Kleiman 1967; Zimen 1974). In areas such as the AOSERP study area, where the primary prey is sedentary, wolf packs establish generally exclusive territories (Mech 1970). Intruding wolves are usually attacked or greeted in an unfriendly manner whenever contacted by a resident pack (Mech 1966). Neighbouring packs establish their territories at least partly through an abundance of scent-marking locations positioned at frequent intervals along the territory boundary (Peters and Mech 1975) and may also advertise the territory through howling (Joslin 1967; Theberge and Falls 1967). It is within these established territories that the pattern of each pack's movements will vary. The nature and local behaviour of the primary prey species of a particular wolf population influences the distribution and movements of the wolves associated with the prey. Although a seasonal shift in habitat selection of moose occurs (Hauge et al. in prep.), the population of this major prey species of the wolves in the AOSERP study area is relatively sedentary; therefore, the literature pertaining to wolves associated with similar prey populations are most relevant to this review.

5.1.1 Winter Habitat Use and Movements by Wolves

During winter, wolves are dependent upon large ungulate prey because most of the smaller animals are unavailable at that time (Keith 1974). Consequently, the wolves wander extensively while searching for sufficient prey. Several studies have indicated the importance of ridges, trails, seismic lines, lake shores, and frozen lakes and rivers as hunting corridors for travelling wolf packs (Stenlund 1955; Mech 1966; 1970; Peters and Mech 1975). The consistent use of the same avenues of travel is apparently governed by topography (Stenlund 1955).

Wolves in a pack do not follow a specific circuit within their territory, but instead usually make irregular movements (Thompson 1952) with no predictable pattern (Kolenosky 1972). However, concentrations of prey, such as deer in deer yards (Kolenosky 1972; Mech 1977a, b) or moose seeking refuge from wind in swamps (Mech 1966), are preferred hunting areas for wolves. Compression of a wolf pack's home range, or even that of a large segment of a population, has been recorded for wolves in winter as a result of prey concentration, particularly for prey that undergo considerable migrations (Cowan 1947; Kuyt 1972). Trespassing into other packs' territories occurs more frequently during winter than summer (Mech 1977b; Stephenson 1978), which may reflect a decreasing availability of prey at that time. Kolenosky (1972) indicates that a major preferred area within one pack's home range in Ontario may have been traditonal; no apparent reason could be determined for the wolves concentrating in this preferred area which had been a wintering area for deer 5 years previously.

Pack movements in winter are quite extensive. Mech (1966) recorded movements of 14.4 km/day including kill time and 50 km/day when just travelling. Stenlund (1955) reported a wolf pack in Minnesota moved 56 km overnight. In Ontario, wolves in one pack travelled an average of 7.1 km/day (Kolenosky 1972).

5.1.1.1 Winter habitat use and movements by wolves in the AOSERP study area. Fuller and Keith (in prep. d) report that wolves in one pack were tracked daily during mid-winter of one year. The wolves travelled at the rate of 9.0 km/day. The pack's winter range was 1,700 km^2, much larger than the summer range of 1,000 km^2. Fuller and Keith (in prep. d) do not indicate whether there was any concentration of activity by the wolves in preferred areas of the home range. Wolves were located in two major habitat types at frequencies that corresponded closely with the availability of those habitats in the study area (Hauge et al. in prep.). However, there was a distinct selection of lowland areas as kill sites; 10 of 11 moose kills were made in lowland areas (Fuller and Keith in prep. d). Lowland riparian habitats are favoured by moose during the winter. Ten percent of all relocations of radio-collared wolves were on cutlines, which reflects the easier travel through the snow there.

5.1.2 Summer Habitat Use and Movements of Wolves

Summer movements of wolves are more restricted than in winter and centre around den sites and rendezvous sites (Mech 1970; Carbyn 1974; Stephenson 1974; Carbyn et al. 1975). Den sites are critical habitats and their suitability governs the success of breeding for that season.

There is a marked shift in the proportions of specific prey items in the summer diet of wolves (Mech 1970). This shift is related to the establishment of the restricted pup-rearing sites. The summer diet is often a direct result of the availability of prey species near the rearing areas. Proximity of rearing areas to active beaver colonies (Theberge et al. 1978) and to ground squirrel colonies (Theberge and Cottrell 1977) may be important factors in the selection of the site and the subsequent success of pup-rearing.

The primary functions of den sites and rendezvous sites are to provide secure places which are suitable for rearing of pups. Den sites are utilized until pups are 8 to 10 weeks of age (Joslin 1967; Mech 1970) while rendezvous areas are used until pups are about 5 or 6 months old, at which age they are capable of keeping up to the wolf pack during its travels for prey (Mech 1970). Characteristics of each type of area and the fact that the pack members must focus their attention on a single location, from which they conduct hunting forays, suggest that dens and rendezvous sites are critical sites.

Dens of many descriptions have been reported. While excavations in soil are the most common type of den, adult wolves will also use the bases of fallen trees, hollow logs, rock crevices, and even shallow depressions or pit dens. Stephenson (1974) found that a majority of the dens examined in arctic Alaska were characteristically excavated in well-drained, usually sandy, soil and situated on a moderate to steeply banked, south-facing slope near a source of water. The presence of permafrost may have largely determined these particular features of slope, aspect, and drainage; however, dens at any latitude must presumably remain dry during their period of use. Therefore, selection of den sites is not likely to be haphazard. Sites suitable for denning are relatively rare; therefore, den sites are commonly traditional (Mech 1970; Stephenson and Johnson 1972).

Each pack may have more than one den in its territory, but this may not indicate a surplus of dens since normal behaviour can include moving the pups as many as three times before finally moving to the rendezvous areas. Such moves may be as far as 2.8 km (Joslin 1967). Den movements have been known to occur as a result of human disturbance (Joslin 1967; Carbyn 1974), or disturbance by bears (Joslin 1967), but in many reported cases no discernible cause for the move could be determined (Stephenson 1974). The potential for early pup mortality during den moves which the adults are forced to make could be expected to rise considerably; however, mortality may not result directly from den disturbance (Mech 1970).

Rendezvous sites are also pup-rearing areas, but because they are larger areas (0.002 km^2 to 0.64 km^2) (Kolensky and Johnston 1967) and wolves will respond more readily to imitations or tape-recordings of howls while at rendezvous areas than at the dens (Joslin 1967), the importance of rendezvous sites has been more intensively investigated (Joslin 1967; Pimlott et al. 1969; Mech 1970).

Joslin (1967) found all rendezvous sites that he observed were located near bogs with open water or lakes. Only in one case (out of 11 sites) was the field of view from the site greater than 100 m. Rendezvous sites located by Kolenosky and Johnston (1967) were located near open water also (swamps and beaver ponds). There does not appear to be selection for a specific type of canopy but an open understory of grass and sedges seems to be preferred (Joslin 1967; Kolenosky and Johnston 1967).

Hunting forays by adult wolves will extend for up to 13 km from a rendezvous site, although the wolves may generally hunt little more than 3 km from the site (Van Ballenberghe et al. 1975). This reduced mobility has been reflected in a change in the proportion of prey items in the summer diet as compared with the winter diet (Frenzel 1974).

Wolves are somewhat restricted in their summer movements by the need to regularly return to pup-rearing areas. Beaver, snowshoe hare, sciurids, birds, and microtines are the secondary diet items which are important during summer (Mech 1970). The proportion of these items in the diet is largely dependent upon local abundance and availability and, therefore, often varies within years among rendezvous sites and between years for the same sites (Voigt et al. 1976; Theberge et al. 1978). Use of non-ungulate food source concentrated near a den or rendezvous site, such as a ground squirrel colony (Theberge and Cottrell 1977) or an abundance of beaver lodges (Voigt et al. 1976) may be extremely important in the rearing of pups when the pack has to be relatively stationary.

The members of an individual pack may make several moves from one rendezvous area to another during the summer (Joslin 1967; Pimlott et al. 1969; Mech 1970). Such moves may be crucial to the success of the pack during pup-rearing by allowing them to move closer to a large kill (Joslin 1967), or to another concentration of prey and may be as far as 9 km (Kolenosky and Jonhston 1967). Disturbances which occur at an inappropriate time may stress the wolves, while effective or actual removal of the preferred habitat used for rendezvous areas may limit the recruitment into the wolf population.

5.1.2.1 Summer habitat use and movements by wolves in the AOSERP study area. Investigations in the AOSERP study area have apparently recorded only one den site and two rendezvous sites (Fuller and Keith in prep. d). While the composition of the summer diet was studied through analysis of scats collected from these sites, no locations or descriptions of the areas were presented nor were observations on behaviour of the pack made during the pup-rearing stage. There appeared, however, to be a positive correlation between the proportion of beaver in the scats from the rendezvous sites and the abundance of active beaver lodges near the sites (Fuller and Keith in prep. d).

5.2 POPULATION DYNAMICS

The population parameters that relate to an understanding of population dynamics of the wolf are density, natality, mortality, age and sex composition, and predator-prey relationships. The ultimate synthesis of this information should clarify the factors involved in population regulation of wolves, as far as they are known.

The universal variables of a predator-prey system are predator density and prey density. Yet there are few investigations of wolf biology which have examined both variables concurrently. Such densities have been the "major stumbling blocks" in efforts to understand the impact that wolves have upon their prey (Pimlott et al. 1969).

5.2.1 Population Density of Wolves

Territory sizes, number of wolves in a pack, and proportion of the population that is composed of lone wolves would together indicate density of wolves in an area. A wide range of densities have been recorded for a number of North American wolf populations (Table 9). There is also considerable variation in pack sizes which have been reported for various North American wolf populations (Table 10), although the majority of packs have between two and eight wolves. Low wolf density areas generally correspond to areas with low mean pack sizes, while the converse is also true (Rausch 1967; Zimen 1974).

Table 9. Wolf population densities reported in North America.[a]

Location	Area (km^2)	Primary Prey Species[b]	Wolf Density (km^2/wolf)	Source
Isle Royale, Michigan	544	moose (1.2 - 1.8/km^2)	18 - 26	Mech (1966); Jordan et al. (1967)
Isle Royale, Michigan	544	moose	12	Peterson (1976)
Algonquin Park, Ontario	1,610	white-tailed deer (4 - 8/km^2)	26	Pimlott et al. (1969)
Ontario	16,100	white-tailed deer	260 - 520	Pimlott et al. (1969)
Minnesota	6,450	white-tailed deer	26	Olson (1938)
Minnesota	10,619	white-tailed deer	44	Sterlund (1955)
Minnesota	10,886	white-tailed deer	27	Mech (1973)
Minnesota	1,857	white-tailed deer	24	Van Ballenberghe et al. (1975)
Wisconsin	390	white-tailed deer	104 - 130	Thompson (1952)
Unit 13, Alaska	51,800	moose	130	Rausch (1967)
Unit 13, Alaska	16,655	moose	153 - 303	Stephenson (1978)
Southeast Alaska	19,425	moose	65 - 104	Atwell et al. (1963)
Prince Albert National Park, Saskatchewan	ND[c]	elk/moose/deer[c, d]	104 - 215	Banfield (1951)
Riding Mountain National Park, Manitoba	ND	elk (1.0 - 1.8/km^2)	25 - 44	Carbyn (1977, 1978)

[a] Data on wolves whose primary prey is relatively sedentary.
[b] Density in brackets where known.
[c] ND = No data.
[d] Prey varied in different parts of park.

Table 10. North American wolf packs reported in the literature -- number of wolves per pack, and pack territory sizes.

Location	PACK SIZE Mean	PACK SIZE Range	Territory Sizes of Individual Packs, km² (number in pack)		Source
Algonquin Park, Ontario	6.0 (21)	3 - 9	129.5 (8)	155.4 (5)	Pimlott et al. (1969)
			103.6 (6)	310.8 (9)[a]	
Riding Mountain National Park, Manitoba	ND[b]	ND	104 to 545		Carbyn (1978)
Alaska	4.1 (236)[c]	2 - 12	ND		Kelly (1954)
Alaska	3.4 (837)[c]	2 - 21	ND		Rausch (1967)
Isle Royale	15 - 16 (1)	11 - 22	272		Mech (1966); Wolfe and Allen (1973)
Superior National Forest, Minnesota	8 (5)[d]	5 - 10	145 (9)	140 (8)	Van Ballenberghe et al. (1975)
			93 (8)	52 (5)	
			122 (10)		
	6.5 (6)[e]	5 - 8	88 (8)	148 (6)	
			153 (5)	194 (8)	
			225 (5)	244 (7)	
Superior National Forest, Minnesota	5.7 - 8.6 (39)[f]	4 - 14	125 to 310		Mech (1977c)
Superior National Forest, Minnesota	2.9 (6)	2 - 7	ND		Stenlund (1955)

[a] This territory apparently belonged to two packs that coalesced.
[b] ND = No data.
[c] Observation of two or more wolves in groups.
[d] Average territory and pack sizes for packs in high prey density areas.
[e] Average territory and pack sizes for packs in low prey density areas.
[f] Average mid-winter pack size for population prior to major decline.

The wide variation in density estimates and pack size probably reflects the fact that different quality ranges will support different densities of the major prey species (Mech 1970). Stenlund (1955) indicated that the wolf population in the Superior National Forest, Minnesota, was stable for 5 years, but within the entire forest the local density of wolves varied; in natural, uncut areas wolf abundance was very low while in cutover areas wolves were common. The white-tailed deer also had lower abundance in uncut areas than in cutover areas; therefore, the wolf population density was apparently responding to the density of white-tailed deer, the major prey.

Wolf density has also been shown to fluctuate with large-scale changes in the density of deer in part of the Superior National Forest, Minnesota (Mech 1977a, b, c). The wolves declined from a high, mean mid-winter pack size of 8.6 to a low mean spring pack size of 3.2 during a period of rapid decline in the deer population. One pack was shown to have declined from nine wolves to only two, the socially dominant alpha-pair, over the years of the prey decline. Even this extensive study in Minnesota did not include consistently thorough surveys of prey density. Therefore, it is not surprising that after more than a decade of extensive and intensive studies of the wolf-prey system, no conclusive statement has been made regarding the numbers of wolves that would be expected to be supported by a particular number of prey.

5.2.1.1 Population density of wolves on the AOSERP study area. Fuller and Keith (in prep. d) attempted to determine wolf densities, pack sizes, and pack territory distribution for the AOSERP study area. Based upon an unspecified number of locations over 1 year a boundary was delineated with apparent confidence for only one wolf pack. A peripheral pair were located by radio-tracking for more than 8 months, but no firm territory boundaries were established. A third pack had been located by radio-tracking for about 1 month during the winter; no boundary lines were firmly established. The fourth pack identified was observed a few times, but no radio-tracking was done on this pack.

The "best estimate" of the wolf population in the AOSERP study area was a minimum of 150 wolves (Fuller and Keith in prep. d). There was no indication of the proportion of lone wolves in the population. The overall density based on this population estimate was 1 wolf/165 km^2. This density is lower than a number of those recorded in the literature (Table 9), but is within the range of those densities.

The pack numbers and territory sizes were estimated from trapper survey responses, radio-tracking records, and general observations (Table 11). The number of wolves in the packs varied from 2 to 16, with most packs having between 6 and 10 wolves; the mean pack size was 8.4 wolves. This mean pack size is larger than most reported (Table 10); it is, however, comparable to that observed in wolf populations inhabiting the region of the highest wintering deer density in the Superior National Forest, Minnesota (Van Ballenberghe et al. 1975).

5.2.2 Natality

Factors which are important determinants of natality are: age at which first breeding occurs; age at which last breeding occurs; proportion of breeding females within the reproductively mature population; and the number of young that potentially can be produced per breeding female.

Not all wolves breed. Wild wolves are not reproductively mature until their second year (Rausch 1967; Mech 1970). The age at which last breeding occurs is unknown, although it is suggested that both old and young wolves have lower litter sizes than do middle-aged female wolves (Stephenson and Johnson 1972). Unless a pack is very large, it usually has only one female producing a litter each year (Rausch 1967; Mech 1970). The overall proportion of mature female wolves that breed varies from one population to another (Keith 1974). In an Alaskan wolf population that was heavily trapped and hunted, 89 percent of the adult females had been pregnant (Rausch 1967), while the mean pregnancy rate of an unexploited wolf population in Algonquin Park, Ontario was 59 percent of adult mature females (Pimlott et al. 1969). The same

Table 11. Number of wolves per pack and pack territory sizes in the AOSERP study area.[a]

Pack Location	No. Wolves in Pack[a]	Territory Size of Pack[b] (km^2)	Basis for Boundary and Pack Size Estimate
Muskeg River	10	1,700	radio-tracking
Syncrude Lease	8	1,443	radio-tracking, observation, trapper survey
Birch Mtns.-Athabasca R.	10	1,642	observations, trapper survey
Birch Mtns.-east	2	1,352	observations, trapper survey
Fort McMurray-west	6	1,761	observations, trapper survey
Clearwater R-Athabasca R. Jcn.	6	1,134	observations, trapper survey
Louise Creek	2	1,000	radio-tracking, observations, trapper survey
E of Muskeg R.	5	ND[c]	observations, trapper survey
NE of Firebag R.	5	ND	observations, trapper survey
Firebag R.-Athabasca R. Jcn.	6	ND	observations, trapper survey
N of Birch Mtns.	10	ND	observations, trapper survey
Dover Lake	10	ND	observations, trapper survey
Fort McMurray-east	16	ND	observations, trapper survey
Athabasca R.-MacKay R-west	6	ND	observations, trapper survey
Athabasca R.-southbend	10	ND	observations, trapper survey
SW of Fort McMurray	9	ND	observations, trapper survey
S of Clearwater R.	9	ND	observations, trapper survey
E of Clearwater R.	6	ND	observations, trapper survey

[a] From Figure 3 in Fuller and Keith (in prep. d).

[b] Measured from Figure 3 in Fuller and Keith (in prep. d) for those packs with circumscribed boundaries for their territories.

[c] ND = No data.

behavioural patterns which help to maintain group cohesion and to reduce intraspecific strife are involved in inhibition of breeding (Kleiman 1967). Socially dominant wolves inhibit the mating of socially inferior, reproductivity mature individuals of the same sex (Rabb et al. 1962; Rabb et al. 1967).

The average litter size reported for wolves is between 4 and 6.5 (Mech 1970) (Table 12). However, some of these records include some *in utero* or postnatal mortality. Two-year old female wolves have a lower average litter size (5.3 fetuses) than adults (6.5 fetuses) (Rausch 1967). Nevertheless, the potential litter sizes (as determined by fetuses, placental scars, or corpora albicantia) are quite high for all female wolves. Indeed, the potential rate of reproduction is far greater for the wolf than for its ungulate prey (Rausch 1967).

5.2.2.1 Natality of wolves on the AOSERP study area. The number of pups produced by three packs on the AOSERP study area was indicated by summer observations. One pair apparently raised three pups, one pack of four adults produced six pups, while a third pack, also containing four adults, produced five pups (Fuller and Keith in prep. c, d). From these observations the average litter size was calculated to be 4.6 pups; this range is well within the range of litter sizes reported from the literature. No further productivity information is available for the AOSERP study area.

5.2.3 Mortality

Mortality of wolves occurs by a number of means and differs for different age groups in different populations or even the same populations at different times (Rausch 1967; Mech 1970). Since the potential rate of reproduction may be constant for all similarly aged wolves in different populations, it is through mortality that the balance between predator and the abundance, quality, fecundity, and availability of prey is maintained. As indicated above, the potential rate of reproduction is considerably higher for wolves than their ungulate prey, so that high *in utero*

Table 12. Average litter sizes reported for wolves in North America.[a]

Location	Number of Litters	Average Litter Size	Range	Information based on	Source
Western Canada	4	5.0	4 - 7	pups	Cowan (1947)
Alberta	3	4.7	4 - 5	pups	Soper (1942)
Northwest Territories	5	4.0	3 - 6	pups	Kelsall (1968)
Thelon River, N.W.T.	18	5.8	2 - 8	fetuses	Kuyt (1972)
	ND[b]	3.5	ND	pups	
Ontario	17	4.9	3 - 7	placental scars, corpora albicantia	Pimlott et al. (1969)
Minnesota	8	6.4	4 - 9	pups	Stenlund (1955)
Alaska	6	5.0	4 - 6	pups	Murie (1944)
Alaska	33	5.5	4 - 8	fetuses	Kelly (1954)
Alaska	175[c]	6.5	3 - 11	fetuses	Rausch (1967)
Alaska	69[d]	5.3	ND	fetuses	Rausch (1967)
Arctic Alaska	43	5.2	1 - 9	pups	Stephenson and Johnson (1972)

[a] Partly adapted from Mech (1970).
[b] ND = No data.
[c] From wolves 3 years old and older.
[d] From 2 year old wolves.

and postnatal mortality must occur or else the wolf would rapidly overwhelm its prey (Rausch 1967).

The number of pups which survive varies with the abundance of prey. During a decline in the deer population of the Superior National Forest in Minnesota, it was apparent that survival of wolf pups was positively correlated with the number of deer consumed during the previous winter, and also declined (Mech 1977b). On Isle Royale, there were more pups observed during winters after high twinning amongst the moose than during low twinning years (Jordan et al. 1967).

There are a number of mortality factors to which wolves are susceptible: diseases, parasites, physical disorders, hunting accidents, intraspecific conflicts, malnutrition, trapping, and hunting. Rabies has been suggested as a population control mechanism in wolves (Cowan 1949), but data supporting this have not been found (Rausch 1958). There is also little evidence indicating that other diseases, including canine distemper, occur at any significant level (Mech 1970). Internal helminth parasites are common in wolves (Stenlund 1955; Mech 1970); in Alberta, a sample of wolves from forested regions showed 98 percent of all wolves had some degree of infection, while many had multiple species infections of at least potentially pathogenic helminths (Holmes and Podesta 1968). Ectoparasites can have considerable effect on wolves, particularly the mite causing mange (Mech 1970); this parasite also occurs in considerable numbers among wolves in Alberta (Carbyn 1974). However, the degree of mortality arising from parasites is unknown for any wolf population. Except in occasional cases of mange outbreak, there is probably not a significant number of deaths attributable to parasitism. A number of other diseases and physical disorders have affected wolves in captivity and wild wolves may also be susceptible to these pathological conditions (Mech 1970); such mortality factors are generally widespread.

During hunting, wolves are susceptible to damaging blows from their prey. Many healed or healing fractures were found among a collection of wolf skeletal material in Alaska (Rausch 1967);

moose was the major prey species of those wolves and direct mortality attributable to injuries inflicted by moose (Stanwell-Fletcher 1942; Jordan et al. 1967). It is likely that such injuries would be more common where the major prey species is as large and formidable as the moose.

Intraspecific conflicts have been responsible for some deaths of wolves, although under normal circumstances such interactions are probably avoided (Mech 1970). Situations of considerable social disruption, resulting in pack reorganizations and changes in territory boundaries, may result in more frequent agonistic encounters. On Isle Royale, the death of a long time alpha or dominant male was followed by disruption of the large pack; shortly afterward frequent observations were made of wolves which had apparently been injured during agonistic encounters with other wolves (Wolfe and Allen 1973). Similarly, intraspecific encounters increased greatly during a decline of the deer prey in the Superior National Forest, Minnesota, and trespassing animals were frequently killed (Mech 1977c); malnutrition and intraspecific strife accounted for 58 percent of the mortality in that wolf population. Malnutrition, in itself, is an important mortality factor of wolves. Its effects are an important facet of predator-prey systems discussed below.

Hunting and trapping can have considerable effect on wolf populations and in some areas these are the major mortality factors (Rausch 1967; Hinmen 1976; Rausch and Hinman 1977). Exploitation of wolves stimulated increased survival of pups to winter but it also increased the mortality of adults and the post-rearing mortality of pups (Rausch 1967). Hunting contributed to a decline of wolves in Wood Buffalo National Park; less hunting of wolves in one part of the park may have contributed to the maintenance of a stable population (Fau 1977). Considerable human-caused mortality occurred of both wolves wandering from the Superior National Forest and of wolves within the forest; of this mortality, approximately 73 percent was by trapping or shooting (Van Ballenberghe et al. 1975). Stephenson (1978) estimated that roughly 75 percent of one year's increment of wolves in a region of Alaska was removed by humans. It is generally accepted that wolf populations can withstand considerable mortality and still maintain population size (Theberge 1975; Hinman 1976; Stephenson 1978). Populations of wolves have been greatly over-exploited in regions of Alaska, but have increased dramatically to near former levels within 15 years after hunting and trapping had been banned (Rausch 1967).

5.2.3.1 Mortality of wolves in the AOSERP study area. Fuller and Keith (in prep. d) document some mortality for the AOSERP study area wolf population. One adult wolf apparently starved, another apparently was an alien and likely killed in an intraspecific conflict, while 51 additional wolves were taken by trappers over a 3 year period. Based on the population estimate for the study area, about 10 to 13 percent of the wolf population is killed annually through trapping (Fuller and Keith in prep.d).

5.2.4 Age and Sex Structure of Wolf Populations

The age structure of a population provides an indication of the level of annual recruitment to the population. The sex structure of a population may have considerable influence upon the natality of that population. Both of these population parameters are difficult to determine for wolves but a few studies that have been reported have indicated that these parameters vary considerably for different populations (Mech 1970).

The age structures, determined largely by skeletal means, for several wolf populations indicate that the proportion of pups is lower in naturally controlled populations than in exploited populations (Table 5) (Mech 1970). In a study in Algonquin Park, Ontario, it was shown that the ratio pups:yearlings:adults differed significantly in the older two age classes for the same population in different years (Pimlott et al. 1969). When this population was under constant predator control pressure, the ratio was 35:40:25, while after 6 years of protection from trapping and hunting the age ratio was 31:17:52. This shift in age structure would appear to indicate that there is increased survival of pups to the yearling stage in an exploited wolf population.

Table 13. Age ratios reported for North American wolf populations.

Location	Natural Condition (N) or Exploited (E)	PERCENTAGE OF POPULATION IN AGE GROUP[a] Pups	Yearlings	Adults	Source
Algonquin Park, Ontario	N	31	17	52	Pimlott et al. (1969)
	E	35	40	25	
Superior National Forest, Minnesota	E	40	29	31	Van Ballenberghe et al. (1975)
Wood Buffalo National Park, N.W.T./Alberta	N	20	ND[b]	80	Fuller (1955); Fuller and Novakowski (1955)
	E	55	ND	45	
Great Slave Lake, N.W.T.	N	13	ND	87	Kelsall (1968)
	E	73	ND	27	
Alaska	E	45	ND	55	Rausch (1967)
Alaska	E	43	ND	57	Stephenson (1978)

[a] Adult age group includes yearlings, except where indicated.
[b] ND = No data.

The sex ratio of wolf populations has been found to be close to 1:1 for nearly half of the studies reported, but for most of the other studies there has been a definite bias in favour of males (Mech 1970). Stenlund (1955) found that males comprised 60-64 percent of the wolves in a Minnesota population and that there was no indication of sex-differential in mortality resulting from hunting or trapping methods which could explain the increased proportion of males. More males than females may be one means of natural control within a wolf population (Stenlund 1955). Furthermore, there is an indication that males may wander more extensively than females (Pulliamere 1965). Each wolf pack also has a basic sex and age structure. In most cases, the pack appears to be a family unit with a pair of adults, the alpha male and female, which breed, and their offspring (Rausch 1967; Mech 1970). There may also be one or two non-breeding adults or, more likely, yearlings in the pack which are also believed to be offspring of the alpha individuals (Mech 1970). In large wolf packs there may be more than one family unit (Mech 1966).

5.2.4.1 Age and sex structure in the AOSERP study area. Fuller and Keith (in prep. d) did not obtain adequate information to determine the sex or age ratio for the population. Wolf pack structure and production seemed to support the single family unit concept of pack organization.

5.2.5 Predator-Prey Relationships

The major prey item in the diet of all North American wolf populations is a single large ungulate species (Pimlott 1967; Mech 1970; Keith 1974). A complex social system and specialized agonistic/submissive behaviour patterns have evolved to maintain the stable social hierarchy, the division of labour, and the group hunting efficiency necessary to hunt such large prey (Kleiman 1967). In becoming adapted to large prey species the wolf has also become associated with prey species whose populations are relatively stable compared with smaller mammals. Any unusual or artificial change in the stability of this prey population might be expected to influence the wolf population.

In Prince Albert National Park, Saskatchewan, moose were seen far more frequently than either elk or deer, both of which comprised substantial proportions of the diet (especially elk), yet moose remains occurred as a trace in scats (Carbyn et al. 1975). Therefore, the relative ease with which elk and deer are preyed upon compared to moose, results in higher predation upon them, despite the higher abundance of moose.

The moose is a formidable prey species; the predation efficiency of wolves hunting moose on Isle Royale was 7.8 percent; i.e., 6 moose were killed out of 77 tested by the wolves (Mech 1966). In contrast, the predation efficiency of a pack of wolves hunting deer in Ontario was 46 percent (Kolenosky 1972). As a result of the formidability of moose, there is significant selection for young, old, or debilitated individuals by wolves. Moose calves, during the summer, are preyed upon significantly more than their proportion of the population would indicate (Rausch 1967; Frenzel 1974; Stephenson 1978). The Isle Royale studies have indicated that, of adult moose, those from 1-5 years are the least vulnerable while those from 8-15 years are the most vulnerable to wolf predation (Mech 1966). In contrast, Stephenson and Johnston (1972) report that a high nutritional content in fat marrow of wolf-killed moose as well as other observations indicated that wolves were not restricted to young or debilitated moose as prey.

During the winter, wolves prey almost exclusively upon the large ungulate prey species; during the summer, they prey on a greater variety of species and a reduced dependence on ungulates is observed (Mech 1966; Keith 1974; Frenzel 1974).

The impact of the wolf upon the primary prey population may be of major significance. The kill rate of prey by wolves is the most meaningful statistic to relate predator to prey consumption. Mech (1966) found that on Isle Royale a large pack of 15 or 16 wolves would kill one moose every 3 days during the winter. Small packs on Isle Royale appeared to be intermediate in feeding success between the large pack and lone wolves (Jordan et al. 1967). Stephenson (1978) suggests that when assessing the impact of wolves

Table 14. Proportions of various food items reported in diets of North American wolves.

		PERCENT OF DIET COMPOSED OF SPECIFIC FOOD ITEMS											
Location	Season[b]	Moose	White-tailed Deer	Elk	Caribou	Beaver	Snowshoe Hare	Other Small Mammals	Birds	Other Animals	Vegetation or Soil	Information Based Upon	Source
Isle Royale, Michigan	W/S	76	0	0	0	11	3	0	1	1	8	scat analysis	Mech (1966)
Kluane National Park, Yukon Territory	S[c]	49.0	0	0	0	4.8	0	37.1	0	9.2	0	scat analysis	Theberge and Cottrell (1977)
	S[d]	54.6	0	0	0	18.8	8.8	4.7	0	12.1	0	scat analysis	
Southcentral Alaska	S[e]	28.3	0	0	4.5	32.5	30.5	1.7	1.7	0.6	0	scat analysis	Stephenson (1978)
	S[f]	52.2	0	0	0	33.3	3.6	0	0	9.4	1.4	scat analysis	
Superior National Forest, Minnesota	S	13.6	56.9	0	0	9.4	3.0	3.6	tr.	6.9	6.6	scat analysis	Van Ballenberghe et al. (1975)
	W	21	66	0	0	ND	ND	ND	ND	ND	ND	scat analysis[g]	
Superior National Forest, Minnesota	W	0	80.4	0	0	0	7.8	7.8	5.9	3.9	0	stomach analysis[h]	Stenlund (1955)
Wisconsin	W/S	0	97	0	0	0	5	3.8	0.5	0.5	27	scat analysis[i]	Thompson (1952)
Prince Albert National Park, Saskatchewan	S	tr.	29[j]	54	tr.	11	3	3	0	0	0	scat analysis	Carbyn et al. (1975)
Algonquin Park, Ontario	S[k]	5 - 15	33 - 76	0	0	7 - 55	tr.	7 - 11	tr.	0	0	scat analysis	Voight et al. (1976)
Algonquin Park, Ontario Ontario	S	8.5	80.5	0	0	7.1	0.6	0.9	0	2.4	0	scat analysis	Pimlott et al. (1969)
	W	0.6	99	0	0	tr.	0	tr.	0	0	0	kill remains	
Pakesley, Ontario	S	2	11	0	0	75	tr.	12	tr.	0	0	scat analysis	Voigt et al. (1976)
Pakesley, Ontario	S	1.4	27.3	0	0	59.3	3.2	0	0	8.8	0	scat analysis	Pimlott et al. (1969)
Marten River, Ontario	S	18	1	0	0	74	tr.	7	tr.	0	0	scat analysis	Voigt et al. (1976)
Marten River, Ontario	S	17.3	42.2	0	0	37.3	0.5	0	0	2.9	0	scat analysis	Pimlott et al. (1969)

[a] For wolf populations whose major prey items are relatively sedentary.
[b] Season for which food habits studied: S = summer; W = winter; W/S both winter and summer.
[c] Onion deer reported by Theberge and Cottrell (1977).
[d] Kathleen den reported by Theberge and Cotrell (1977).
[e] From scats collected near den.
[f] From scats collected near a rendezvous site.
[g] Only 69 scats collected in winter.
[h] Percent of stomachs in which food item found.
[i] Percent of scats in which food item found.
[j] Includes both mule and white-tailed deer.
[k] Ranges for four years' data.
tr. = trace.

on prey, changes in the number of functional packs is an area probably more important than changes in the number of wolves.

The influence of wolves on a prey population can also be approached from an estimate of average consumption per wolf. Kuyt (1972) calculated that captive wolves fed on bison meat and dog food in the Northwest Territories consumed 1.6 kg/wolf/day or 0.05 kg/kg of wolf/day, which is probably the minimum maintenance requirement for wild wolves. Pimlott et al. (1969) calculated from Mech's (1966) figures that wild wolves on Isle Royale consume 4.5 kg/wolf/day or 0.13 kg/kg of wolf/day. Wolves can adjust to a wide variation in the availability of food, and can consume up to three times their minimum maintenance requirement (Mech 1977b). This additional consumption is apparently required by each individual of a pack to ensure survival and the successful rearing of pups during the following season (Mech 1977a, b).

As discussed earlier, the density of the wolf is dependent upon the density of the primary prey species. In effect, the fate of a wolf population is determined by the health of ungulate prey populations (Rausch and Hinman 1977). However, some wolf populations appear to provide a controlling influence upon prey populations, although the wolves may not be the ultimate controlling factor (Mech 1966, 1970). Pimlott et al. (1969) suggest that wolves may be capable of controlling deer populations when the ratio of wolves to deer does not exceed 1:100. However, although Pimlott et al. (1969) agree that under wolf predation the moose on Isle Royale have not overrun their browse vegetation, they consider the data on moose numbers and annual kill rate of moose by wolves to be incomplete and, therefore, do not believe the wolf population necessarily controls the Isle Royale moose population as suggested by Mech (1966).

There are several records of declines in ungulate populations in years of heavy winter snowfall which occurred as a result of increased wolf predation. Wolves are hampered by deep, soft snow, but during late winter the formation of icy crusts are an advantage to the wolves which can run on the snow surface and a disadvantage to their prey which break through the crusts (Mech

1970). In years of deep snow, wolves on Isle Royale increase their kill rate of calves and prime age moose (Peterson and Allen 1974) and there is more wastage of prey. In Alaska, wolves have retarded moose populations, that have been stressed by extreme climatic phenomena, by checking the prey population recovery (Rausch and Hinman 1977). In Minnesota, wolf predation in conjunction with a severe winter first caused a considerable decline in a deer population, followed by a decline in the wolf population itself (Mech 1977a, b, c).

5.2.5.1 Predator-prey relationships in the AOSERP study area. Fuller and Keith (in prep. c. , d) conducted analyses of 1,004 wolf scats which were collected during the summer and late fall at one den site and near two rendezvous sites and recorded wolf kills during two complete winter seasons. The summer food habits, as determined from the scats, were found to vary considerably between the pup-rearing sites. Adult and calf moose were the predominant food items at two sites, a rendezvous site and the den site, while beaver occurred much more frequently in scats from the other rendezvous site. Beaver was of considerable prominence in the scats from the den site and the latter rendezvous site. Other prey items found in the summer diets of wolves at pup-rearing areas were snowshoe hare, muskrat, birds, an alien wolf, vole, squirrels, porcupine, and fish.

On the basis of preliminary census data, Fuller and Keith (in prep. d) indicate that the proportion of beaver in the summer diet was positively correlated with the number of active beaver lodges in the area surrounding the rendezvous sites. They also suggest that the relatively high proportions of non-ungulate prey remains from two sites may be a result of low ungulate availability.

Winter food habits were determined by examining 21 wolf-killed moose (Fuller and Keith in prep. d). Calves comprised 43 percent of these kills, while calves represented only 19 percent of the winter moose population (Hauge et al. in prep.). The average age of adult moose which were killed by wolves was 6.1 years, significantly greater than the 4.8 year average age of the moose population (Hauge et al. in prep.). Three of the wolf-killed moose were apparently debilitated. Therefore, there appears to have been a disproportionate predation of young, old, and unhealthy moose by wolves in the AOSERP area.

Significantly more of the kill sites were located in lowland areas than upland areas; 40-60 percent of moose were distributed in lowland areas during winter (Hauge et al. in prep.). This distribution of kill sites is attributed to the ability of wolves to cope with the deep, crusted snow in the lowlands, compared with the inability of moose to cope with the same snow (Fuller and Keith in prep. d).

From intensive winter investigations of one pack, Fuller and Keith (in prep. d) determined kill rates, average daily consumption, and distance between kills. The pack killed and/or consumed one moose every 4.6 days. Wastage of carcasses was minimal and average food consumption was 6.0 kg/wolf/day or 0.15 kg/kg of wolf/day. The average distance travelled by the pack between kills was 43 km.

Fuller and Keith (in prep. d) present an assessment of the the impact of wolf predation on moose, based on data projected from the mid-winter intensive study of one radio-collared pack. They estimate that wolves killed or scavenged 11 percent of the adult moose population and 31 calf moose in one year. They further calculate that if hunting mortality is greater than 35 percent, the moose population within the pack's territory would decrease; if hunting mortality is less than 35 percent, the moose population would increase. Hauge et al. (in prep.) determined a hunting mortality of 50 percent. Fuller and Keith (in prep.) conclude that wolf predation, in conjunction with existing natural mortality and hunting pressure, could cause a decline in moose numbers in the Muskeg River area of the AOSERP study area. However, moose populations over the entire AOSERP study area appear to be stable or slightly increasing (Hauge et al. in prep.).

5.2.6 Population Regulation of Wolves

Despite a proliferation of extensive wolf population studies over the past decade, there is little agreement on how proximate and ultimate factors affect wolf population regulation (Jordon et al. 1967; Pimlott et al. 1969; Mech 1970; Van Ballenberghe et al. 1975; Mech 1977a, b, c). The population dynamics of each wolf population seem to be influenced differentially by stress, food supply, territoriality, and human exploitation (Van Ballenberghe et al. 1975). Certainly, parameters such as pack density, mean pack size, prey abundance, and human exploitation differ for different populations (Mech 1970), so that a model of population regulation may be unique for each wolf population. As previously discussed, human exploitation can alter wolf population age structures and may locally and temporarily depress wolf populations; however, this is not a regulating mechanism with which wolves have primarily evolved and, therefore, is likely to act extrinsically to the proximate and ultimate regulating mechanisms with which the wolf has evolved. Social factors and food supply are discussed as the ultimate factors in wolf population regulation by wolf ecologists (Jordan et al. 1967; Pimlott et al. 1969; Mech 1970; Van Ballenberghe et al. 1975).

5.2.6.1 Social factors in wolf population regulation. There can be no doubt that social stress and organization have profound effects upon wolf populations. The social organization of wolves into packs has significant bearing upon wolf impact upon prey populations and in areas where the prey is relatively sedentary, has resulted in the establishment of territories.

When population density is high and all suitable habitat is occupied, some individuals may not be able to establish a territory and, consequently, may form a non-breeding surplus, emigrate, or die at a greater rate than successful territory holders; when these conditions are not met, territoriality is unlikely to regulate a population (Brown 1969).

Van Ballenberghe et al. (1975) believe that a significant surplus of non-breeders has never been demonstrated in a dense wolf population. Jordan et al. (1967) consider extra-territorial wolves on Isle Royale to be low order social subordinates or senile individuals. Van Ballenberghe et al. (1975) conclude from this that territoriality itself functions minimally in wolf population regulation. There seems to be a contradiction between Jordan et al.'s (1967) statement and the conclusion reached by Van Ballenberghe et al. (1975). The implication is that social stress is more responsible than territoriality for the non-breeding status of extra-territorial wolves; however, it may be misleading to separate stress and territoriality, for much the same social behaviours function to maintain the sociality of the pack as to maintain the territorial aggression between packs.

Social stress alone apparently has a considerable effect upon wolves. It has been shown for captive wolves and inferred for wild wolves that social interactions lead to inhibition of reproductive behaviour within a pack (Rabb et al. 1967; Mech 1970). In a low-density population in Alaska, Rausch (1967) observed a natality rate of 2.67 pups per adult, while in Algonquin Park there were only 1.11 pups per adult (Pimlott et al. 1969). Mech (1970) suggests that stress factors were responsible for the reduction in potential productivity by 42 percent, and that these stress factors were mediated by proximate factors such as an excess of adult males, a reduced mean litter size, and failure of many adult females to breed.

The disruptive effect of interpack stress on Isle Royale was dramatically demonstrated. After the death of the alpha male of the large pack, which had previously dominated the island's wolf population, a period of interpack strife, and possibly emigration, ended in 2 years with a decline to nearly half the previous fairly stable population level (Wolfe and Allen 1973).

5.2.6.2 Food supply in wolf population regulation. Van Ballenberghe et al. (1975) suggest that food supply has been a primary determinant of the ultimate densities reached by at least three wolf populations: the wolves of Isle Royale, Michigan; of Algonquin Park, Ontario; and of northeastern Minnesota. All three populations approach the density of one wolf per 2.59 km^2 suggested as the maximum for wolf populations by Pimlott et al. (1969).

The Isle Royale wolf population was stable for several years; Mech (1966, 1970) considered that this occurred despite an abundant food supply. Jordan et al. (1967) suggested that pup survival was positively correlated with high twinning rates for moose, and that in years of low moose calf production there was increased starvation of young wolves and the population growth was limited.

The Ontario and Minnesota wolf populations studied had similar food habits, were in areas of similar prey densities, and, despite different age structures, were of similar densities

(Pimlott et al. 1969; Van Ballenberghe et al. 1975). Van Ballenberghe et al. (1975) showed from radio-tracking studies, that territory sizes of packs were compressed, and the number of wolves per pack was greater, in areas with high prey density compared with packs in peripheral areas with low prey density. They suggest that, despite mechanisms of social stress and territoriality that might be expected to operate, reproduction was not inhibited in the crowded areas and large pack sizes occurred. This phenomenon was likely a result of the high numbers of deer concentrating in wintering yards within the wolves' territories along the shore of Lake Superior (Van Bellenberghe et al. 1975). Environments rich in food may lower the thresholds of other regulating influences such as social stress and territoriality (Van Ballenberghe et al. 1975). Mech (1970) suggests that social stress may act in conjunction with food supply. As vulnerable prey grow scarcer in the pack territory, the wolf pack would have to travel further and more frequently. As a result, the possibility of interpack interactions, both direct contact and indirect contact through scent posts, would be increased. Social stress may eventually affect the vigour of a subordinate pack leading to mortality resulting from malnutrition, stress, parasitism, and disease. There seems to be strong evidence for this combination of social factors and food supply in Mech's (1977a, b, c) study in the Superior National Forest, Minnesota. A rapid decline in prey (deer) was followed by a decline in wolves; in the latter stages of the decline, both trespassing and interpack strife had greatly increased to the point where mortality resulting from wolves killing each other was much more common.

5.3 POTENTIAL IMPACTS OF LARGE DEVELOPMENT PROJECTS

A consideration of the potential impact of large development projects must first isolate the various components of the development which could have an impact on any aspect of wolf populations. The development of oil sands involves considerable habitat alteration as a part of the mining process and related developments, increased human activity causing disturbance, and increased exploitation the wolf and its ungulate prey as a result of the enlarged human population base in the area.

5.3.1 Alteration of Habitat

Changes in habitat could affect wolves in a number of ways; however, the basic means is through the direct loss of habitat for pup-rearing areas and through the effect of habitat alteration upon the prey base.

As indicated above, specific requirements exist for den and rendezvous sites and importance of these sites to the success of breeding wolves suggests that the removal of such habitat through development could be critical to a wolf population. Knowledge of the location and abundance of suitable areas for pup-rearing would be useful information for land-use planning; obtaining such knowledge has been considered for different purposes in Canadian National Parks (Carbyn et al. 1975).

A reduction of ungulate prey as a result of development activities might cause a local decline in the number of wolves, a typical predator response. The social infrastructure of a wolf population may result in other responses to actual physical loss of habitat than merely a decline in numbers. Social disruption of wolves in an area has been known to lead to increased intraspecific strife and, at least, a temporary reduction in the wolf population (Wolfe and Allen 1973; Mech 1977c).

Artificially enhanced food supply may occur along with development as a result of a proliferation of dumps. These alternate food sources are known to be attractive to wolves, particularly during winter, and may even become a regular stop on a foraging route (Carbyn et al. 1975; Van Ballenberghe et al. 1975; Grace 1976). Two possible results of the encouragement of use of dumps have been suggested by Grace (1976): the impairment of health and a reduction in the effectiveness of the wolves as predators, which would then reinforce the dump habits; or an increase in the success of the predator and, thus, increased pressure of the predator on the normal prey population. Grace (1976) recommends discouraging use of dumps by wolves because, among other reasons, constant contact with humans may lead to loss of mutual wariness between human and wolf, and may promote situations in which human life is endangered.

5.3.2 Disturbance Factors

In the discussion on summer habitat use, it was indicated that human disturbance may cause wolves to make disruptive moves between dens or rendezvous sites. Carbyn (1974) further documents sensitivity of denning areas by recording the desertion of traditional wolf den sites which were located near different types of development in Jasper National Park, Alberta. However, several active wolf dens can be found within 16 km of the city of Fairbanks, Alaska (Rausch 1967).

Roads are major disturbances and wolves tend to avoid particularly busy highways (Carbyn 1974). However, road-killed ungulates will attract wolves which scavenge on kills and may, themselves, become road mortalities. This is probably not a substantial mortality factor (e.g., one wolf killed per year on roads in Jasper National Park [Carbyn 1974]). However, the high density and high speed of travel of vehicles in the AOSERP study area may be a major disturbance factor for wildlife.

5.3.3 Increased Exploitation

The effects of overexploitation of wolf populations through hunting and trapping are well documented (Rausch 1969; Mech 1970; Rausch and Hinman 1977). Extensive resource development is often accompanied by an increased human population base. Hunting of wolves is rare in Alberta, although trapping netted an average of 562 wolves annually during the period 1970 to 1974 (Renewable Resources Consulting Services Ltd. 1975). Predator control efforts play a major role in reducing wolf numbers locally and temporarily. Typical bounty programs have been notoriously unsuccessful at depressing wolf populations (Mech 1970; Kuyt 1972). Large-scale poisoning programs were largely responsible for early eradication of wolves in many parts of North America (Young and Goldman 1944). However, such programs are conducted primarily in agricultural areas; the AOSERP area lacks agricultural areas.

6. ASSESSMENT OF BASELINE DATA RELEVANT TO LARGE MAMMALS IN THE AOSERP STUDY AREA

6.1 OBJECTIVES

The three basic types of biological data which are required to complete the documentation and evaluation of impacts of oil sands developments on large mammals are:

1. Knowledge of the seasonal population dispersion (including the distribution, habitat use, and movement patterns of individuals of the population);
2. Knowledge of the potential impacts of development projects (including effects of sensory disturbances, agents of direct mortality, and habitat alterations); and
3. Knowledge of the population dynamics (including density, natality, and mortality).

The data available for each species of large mammal in the AOSERP study area will, therefore, be assessed under these three major headings. The adequacy of the available data in each category are summarized in Table 15.

Table 15. Adequacy of available data relevant to the documentation and assessment of the impacts of oil sands developments on large mammals in the AOSERP study area.

Topic	Moose	Woodland Caribou	Wolf
Seasonal Population Dispersion			
Distribution on the AOSERP Study Area	Adequate	Major Gap	Adequate
Habitat Use	Major Gap	Major Gap	Major Gap
Movement Patterns	Adequate	Adequate	Minor Gap
Potential Impacts of Development			
Sensory Disturbances	Major Gap	Major Gap	Minor Gap
Direct Mortality	Minor Gap	Minor Gap	Minor Gap
Habitat Alterations	Adequate	Adequate	Adequate
Population Dynamics			
Density	Major Gap	Major Gap	Major Gap
Natality	Adequate	Adequate	Adequate
Mortality	Adequate	Adequate	Adequate

7. MOOSE

7.1 Population Dispersion

7.1.1 Distribution on the AOSERP Study Area

The knowledge of the distribution of moose over the AOSERP study area is excellent--the moose is known to occur throughout the study area. Therefore, no studies are required to document the distribution of moose on the AOSERP study area.

7.1.2 Habitat Use

As noted in the literature review, the habitat selection patterns of moose do not show significant variation throughout the range of the species; indeed, the data which have been gathered in the AOSERP study area concerning habitat use of moose are generally similar to those reported from elsewhere in the species range. Thus, current knowledge of the general habitat selection patterns of moose on the AOSERP study area is good. However, knowledge of the general habitat selection patterns do not, in themselves, provide an adequate data base for the documentation of impacts.

The number of animals lost to the population as a result of habitat loss will depend on the amount of habitat lost, the season and duration of loss, and the numbers of animals normally using the areas when the habitat is unavailable. Therefore, knowledge of the seasonal density of moose in each habitat type on the AOSERP study area is essential to be able to document the impacts of oil sands development on moose. The data collected within the AOSERP study area concerning the seasonal density of moose in each habitat type are not adequate to complete an assessment of the impact of oil sands development.

The data necessary to determine the level of habitat use is the proportion of time spent in each habitat type by members of a population during each season. The use of any direct observation method (e.g., aerial survey, radio-relocations) to determine the level of habitat use is subject to considerable error since each relocation or observation point consists, in essence, of the fact that an animal was in a specific cover type at a specific time. Therefore, unless continuous records are kept of the location of the animal, the data may not reflect the actual time spent by the animal in each cover type; this is especially true where the relocation points are not taken in a highly systematic manner in all seasons, at all times of day, and in all weather conditions. Additional problems may occur if the data are gathered from a study sample of radio-collared animals which do not reflect the age and sex composition of the general population. The majority of the habitat selection work which has been conducted on the AOSERP study area has been done by means of direct observation.

Nowlin (in prep.) reports on the habitat use of moose in the AOSERP study area as determined by radio-telemetry. This study has several major weaknesses. The study was based upon a total of 95 relocations of six mature moose (four females and two males) during the fall period and 116 relocations of 10 mature moose (seven females and three males) during the winter period. Therefore, the data base of this study must be considered to be extremely limited, and probably inadequate, especially in view of the complicated analysis which was subsequently performed (10 habitat types x 4 categories of use x 2 seasons). Nowlin (in prep.) himself comments on the inadequate sample sizes obtained. The data base consisted of radio-relocations which were gathered only during the daylight period, yet Nowlin (in prep.) shows that moose select different habitat types for bedding than for other activities; therefore, the data do not accurately reflect the daylong level of habitat use. The study population (radio-collared animals) does not appear to reflect the age and sex ratios which occurred in the population, since no calves or yearlings were represented; moreover, the composition of the study sample was itself altered during the course of the study. The accuracy of the radio-relocations points was apparently only to within 30 m; this was often insufficient to accurately place the moose within a specific habitat type since more than one type often occurred with a 30 m radius of the point. The study was conducted only during the fall and winter period and the winter was considered to be atypical due to a lack of snow cover (Nowlin in prep.). Similarly, the moose habitat selection data reported by Hauge et al. (in prep.) suffer from the general problems associated with radio-telemetry studies of habitat use: the relocation data do not appear to have been collected in a systematic manner and are therefore not representative of the entire study period; the numbers of relocations are generally small; and the study population was not representative of the population in the study area.

It should also be stressed that the vegetation of the AOSERP study area had not been mapped at the time when all of the above data concerning moose habitat use were collected. In most instances the habitat types defined during studies of moose habitat use on the AOSERP study area are not equivalent to those which were ultimately mapped by Thompson et al. (1978). Therefore, the habitat use data which are available cannot be strictly related to the existing vegetation maps of the AOSERP study area and, thus, may not be used as the basis for an integrated evaluation of the effects of oil sands development based upon the vegetation maps of the study area.

Because of the problems which are discussed above, we consider that none of the studies which has been conducted to date are adequate to determine the relative level of use of each habitat type by moose on the AOSERP study area. A study is required to fill this data gap prior to completion of a documentation of the impacts produced by development of oil sands areas.

7.1.3 Movement Patterns

The knowledge of movement patterns of moose on the AOSERP study area appears to be adequate for an assessment of the effects of oil sands development. As noted in the literature review (see Section 4.1.2), the movement patterns of moose in the AOSERP study area conform to the basic movement patterns which have been reported for other populations of moose inhabiting areas similar to the AOSERP study area. Therefore, no further data are required to document the effects of oil sands developments on moose.

7.2 POTENTIAL IMPACTS OF DEVELOPMENT PROJECTS

7.2.1 Sensory Disturbances

Knowledge of the reactions of moose to various forms of sensory disturbance appears to be almost totally lacking (see Section 4.2.1). Few quantitative data exist concerning the reactions of moose to various sources of sensory disturbances which will occur during oil sands development (mobile equipment, stationary equipment, human presence). In general, the responses of most species of ungulates to sensory disturbances appear to be basically similar. It is, therefore, unlikely that the reactions of moose to disturbance are substantially different from those of other ungulates (Section 4.2.1). However, the data which are available concerning either the sphere of influence or the magnitude of the effects of various forms of sensory disturbances on moose are not generally adequate to complete an analysis of the effects of oil sands development. As noted in the literature review, sensory disturbances will produce two major effects: (1) alteration of the energy which is expended by the animal as a result of stress reactions; and (2) avoidance of habitat because of intolerable sensory disturbances. It is our opinion that the most significant effect which the sensory disturbances that are associated with oil sands development will produce will be to reduce the availability of habitat due to avoidance of areas by moose. Therefore, we consider that a major data gap exists and that a study should be initiated to document the sphere of influence of various sources of sensory disturbance within which the use of habitat by moose will be affected and the magnitude of the effect of these disturbances. These studies will be required prior to completion of an analysis of the effects of oil sands developments on moose.

7.2.2 Direct Mortality

Direct physical harm causing death of or injury to animals may result from collisions with vehicles, accidents (such as entanglement with wire), contact with or ingestion of environmental contaminants, or the recreational activities of employees of a development project.

The number of animals that are likely to die as a result of collisions, accidents, ingested toxic materials, and hunting induced by a development project cannot be objectively estimated. A guess can, however, usually be supported to some degree by experience with similar projects and a knowledge of population dispersion in relation to the proposed project. For example, it appears that the impacts which highways and similar corridors will have on ungulate populations are a function of the location of the road relative to ungulate habitat and movements as well as the operation and maintenance procedures (see Section 4.3.7.3. Similar relationships likely hold for the other forms of direct mortality; for example, the increases in level of hunting which will occur will be a function of the number of people attracted to the area by the project, the amount of increased access provided by the project, and the location of project facilities relative to areas of ungulate abundance.

Therefore, the ability to be able to estimate the magnitude of the direct mortality which will result from a development project depends primarily upon a knowledge of the seasonal population dispersion and upon experience gained from other projects.

The potential for increased moose mortality resulting from increased recreational hunting can be controlled through the development of appropriate management practices by the responsible provincial government agencies. Therefore, since we do not believe that AOSERP has a mandate to provide data for management purposes, no further research needs to be conducted on this topic. However, if AOSERP is required to provide the data required for the management of moose mortality which would result from the anticipated increase in recreational hunting, then the existing data are not adequate and information concerning the following knowledge gaps is required: (1) the current levels of hunter harvest, (2) the anticipated increase in hunter harvest induced by oil sands developments, and (3) the harvestable surplus of moose on the AOSERP study area.

Thus, although we have identified a minor gap as existing in knowledge of this factor (Table 15) this gap will be adequately filled once additional data concerning the seasonal population dispersion, particularly the habitat use, of moose are collected.

7.2.3 Habitat Alterations

The major types of habitat alterations which will occur on the AOSERP study area will relate to vegetation removal (e.g., clearing and strip-mining); these areas may eventually be reclaimed, producing, in essence, early seral vegetation. Other areas of vegetation destruction (e.g., fire) may not be reclaimed; these disturbances will also result in early seral habitat. It is well known that vegetation alteration which produces early seral habitats typically results in increased local densities of moose once browse production has increased sufficiently (Section 4.1.1.2 and 4.1.1.4). What is not known however, is the efficiency of revegetation with respect to the creation of moose habitat, what effect, if any, moose browsing will have on the success of a reclamation project, and whether moose populations can be enhanced through the selection of an appropriate reclamation plan. We recommend that research be initiated to determine the efficiency of reclamation with respect to the creation of habitat, the effects of moose on a reclamation program, and the effects of the reclamation program on the moose population.

The effect of physical alterations of habitat (e.g., roads) is not well known. However, the major impacts of physical alterations are likely to be due to the associated sensory disturbances. Moose appear to be relatively sedentary, and any movements which occur are undertaken by individual moose rather than in herds as a population. Therefore, the potential for physical alteration to produce barriers to movement of moose or to alter the ability of moose to exploit the habitat is relatively small.

7.3 POPULATION DYNAMICS

7.3.1 Density

The density of moose within the AOSERP study area appears to have been documented only in selected portions of the study area, primarily the Bitumount area and Syncrude Lease No. 17; it appears that there has never been a systematic survey of the entire AOSERP study area. Therefore, the relative density of moose in various portions of the study area is not known. Despite the fact that the data which are available appear to be in close agreement (see Section 4.3.1), we feel the potential for variation in density of moose within the various physiographic regions of the study area, and therefore the potential for variation in the level of impact which would result from development, is sufficient to justify completion of a study designed to determine the relative density of moose within various portions of the AOSERP study area.

7.3.2 Natality

We feel that sufficient baseline data are available concerning the natality of moose to complete an analysis of the impacts of oil sands developments on moose. As noted in the literature review, the productivity of most North American moose populations is relatively similar (see Section 4.3.7.2). The moose is a species which is adapted to the exploitation of rapidly created seral habitats and is capable of rapid recovery from natural or man-induced reductions in population levels; moose populations naturally experience great fluctuations in population density, which appear to be related to the quality of the available habitat (see Section 4.3.1.2). Thus, the productivity of moose populations is potentially great and natality is responsive to changes in habitat availability.

7.3.3 Mortality

The data concerning mortality of moose on the AOSERP study area appears to be adequate to complete an analysis of the impact of oil sands development on moose populations. Fuller and Keith (in prep. a) conclude that hunting accounts for almost all of the mortality, exclusive of wolf predation, sustained by the moose population of the Muskeg River drainage. Since the moose population of the AOSERP study area appears to be stable or slightly declining (Hauge et al. in prep.) it would appear that the population is currently sustaining a maximum level of harvest. Therefore, it appears that a potential exists for overharvest of moose by hunters, particularly in view of the increased human populations in and ease of access to the study area which would result from any development. However, as noted earlier (Section 7.2.2), since regulations could be formulated by the responsible provincial agencies to prevent any such overharvest, we do not feel AOSERP requires further data on this aspect of moose mortality.

7.4 SUMMARY

In summary, we consider that the following data gaps exist, and remain to be filled before a documentation and assessment of the impacts of oil sands developments on moose could be completed:

1. A major data gap exists in knowledge of the seasonal level of use of each habitat type on the AOSERP study area;
2. A major data gap exists in knowledge of the sphere of influence which the various types of sensory disturbances have on moose; and
3. A major data gap exists in knowledge of the relative density of moose in all portions of the AOSERP study area.

It appears that the major thrust of the research which has been carried out on the AOSERP study area has been toward gaining a knowledge of population dynamics of moose. The data on population dynamics of moose are excellent and will allow evaluation of impacts to be completed; however, relatively little effort appears to have been expended in gathering the types of data which are relevent to the inital documentation of the impacts. Therefore, most of the data gaps occur under the topics of seasonal population dispersion and susceptibility to impact from development. Research proposals have been included which will provide data relevant to these gaps.

8. WOODLAND CARIBOU

8.1 POPULATION DISPERSION

8.1.1 Distribution on the AOSERP Study Area

Current knowledge of the distribution of woodland caribou on the AOSERP study area is not adequate to document the impacts which would result from oil sands development. Fuller and Keith (in prep. b) studied the woodland caribou in the Birch Mountains and report that caribou are also present in the extreme southern part of the AOSERP study area; however, occurrence of woodland caribou in the remainder of the study area does not appear to have been documented. We therefore feel that a study should be conducted to document the occurrence of woodland caribou within the AOSERP study area.

8.1.2 Habitat Use

The available data concerning habitat use of woodland caribou in the AOSERP study area are not adequate to complete an assessment of the impact of oil sands development projects. The reasons for this assessment are similar to those outlined in the assessment of adequacy of moose habitat use data (Section 7.1.2): (1) the data were collected by means of direct observation; (2) sample size is limited; (3) data were not systematically collected; (4) the sampling basis (radio-tagged caribou) does not appear to be representative of the entire population in terms of their age and sex ratios; and (5) the vegetation communities used during collection of habitat use data were not those which were ultimately mapped and may not be equivalent to the vegetation communities which were mapped.

However, as was the case for moose, the general pattern of habitat selection by woodland caribou in the AOSERP study area appears similar to that reported from elsewhere in the species range. Thus, the major data gap which remains is to determine the proportion of time which is spent by woodland caribou in each habitat type on the AOSERP study area during each season (seasonal density). However, until the distribution and density of woodland caribou is established for various portions of the study area, we cannot recommend that a woodland caribou habitat use study be conducted; such a study is likely not warranted unless populations of caribou exist in those areas of the AOSERP study area which will be subject to development activities.

8.1.3 Movement Patterns

Current knowledge of woodland caribou movements on the AOSERP study area appears to be adequate for an analysis of the effects of oil sands development. Movements of woodland caribou appear to be relatively small in extent and are undertaken independently by individuals rather than as a herd by the entire population (see Section 3.1.2). Therefore, no further studies concerning movements of woodland caribou are required.

8.2 POTENTIAL IMPACTS OF DEVELOPMENT PROJECTS

8.2.1 Sensory Disturbances

Current knowledge of the reactions of woodland caribou to various forms of sensory disturbance appears to be almost almost totally lacking (see Section 3.2). Considerable quantitative data exist concerning the reactions of barren-ground caribou; however, even for the barren-ground caribou few quantitative data exist concerning the sphere of influence or magnitude of the effects of various forms of sensory disturbance. Moreover, the applicability of behavioural data collected concerning the barren-ground caribou, dwelling in open habitats, to the woodland caribou, dwelling in forested habitats, is questionable. Therefore, a major data gap exists in our knowledge of the effects of sensory disturbances on woodland caribou. Despite the fact that this data gap exists, the requirement for further studies designed to fill this gap cannot be assessed prior to a knowledge of the distribution and density of woodland caribou in the AOSERP area; such studies are likely not warranted if woodland caribou populations are confined to portions of the AOSERP study area which are not likely to be subject to development.

8.2.2 Direct Mortality

As detailed in the section concerning direct mortality of moose (Section 7.2.2), the ability to estimate the magnitude of direct mortality which will result to woodland caribou from oil sands development depends primarily upon a knowledge of the seasonal population dispersion and upon experience gained from other projects.

Any potential impacts which would result to woodland caribou populations from increased recreational hunting could be easily mitigated by the development of appropriate management plans by the responsible government agencies. Therefore, since we do not believe that AOSERP has a mandate to provide data for management purposes, no further research needs to be conducted on this topic. However, if AOSERP is required to provide the data required for the management of woodland caribou mortality which would result from the anticipated increase in hunting, then the existing data are not adequate and information concerning the following knowledge gaps is required: (1) the current levels of hunter harvest; (2) the anticipated increase in hunter harvest induced by oil sands developments; and (3) the harvestable surplus of woodland caribou on the AOSERP study area.

8.2.3 Habitat Alterations

As noted in the section concerning habitat alterations for moose (Section 7.2.3), most habitat alterations on the AOSERP study area will result in seral habitats; it is well established that this will be detrimental to woodland caribou populations (see Section 4.2.3).

The effects of physical alterations, such as roads, is not well known. However, since the major effects of such alterations typically result from the production of barriers to or deflections of movements and since woodland caribou on the AOSERP study area are relatively sedentary (see Section 3.1.2), the potential effects of physical alterations will likely be confined to the loss of habitat required to construct them and the associated sensory disturbances.

Therefore, the data base concerning habitat alterations appears to be adequate.

8.3 POPULATION DYNAMICS

8.3.1 Density

The density of woodland caribou within the AOSERP study area has been documented only for the Birch Mountains area despite the fact that woodland caribou are known to exist elsewhere in the study area (see Section 3.3.1.1). We feel that the potential for variation in density of woodland caribou within the various physiographic regions of the study area, and, therefore, the potential for variation in the level of impact which would result from development, is sufficient to justify completion of a study designed to determine the relative density of woodland caribou within various portions of the AOSERP study area. Moreover, the results of such a study will be required prior to assessment of the requirements for further studies concerning the habitat use of, and effects of sensory disturbances on, woodland caribou.

8.3.2 Natality

Current baseline data concerning natality of woodland caribou are sufficient to complete an analysis of the impacts of oil sands developments. As noted in the literature review (see Section 3.3.2.1), the productivity of woodland caribou populations does not appear to show much variation. Therefore, while little data are available from within the AOSERP study area, natality rates which have been documented for other caribou populations are likely applicable and sufficient.

8.3.3 Mortality

Fuller and Keith (in prep. b) indicate that the woodland caribou population on the AOSERP study area may be declining. As noted in the literature review (see Section 3.3.2.2.3), wolf predation and human hunting are generally thought to be major factors influencing the growth of caribou populations. Fuller and Keith (in prep. a, b) consider predation by wolf is probably a minor mortality factor, while natives from Fort MacKay probably kill no more than 5 to 10 caribou per winter over the entire study area. It appears, therefore, that the current mortality levels of woodland caribou are either at or just above the maximum level which can be supported. Therefore, it appears that a potential exists for overharvest of woodland caribou by hunters, particularly in view of the increased human populations in, and ease of access to, the study area which would result from any development. However, as noted earlier (Section 7.2.2), since regulations could be formulated by the responsible government agencies which would prevent any such overharvest, we feel that no additional data are required by AOSERP.

8.4 SUMMARY

In summary, we consider that the following data gaps exist and remain to be filled before a documentation and assessment of the impacts of oil sands developments on woodland caribou could be completed:

1. A major gap exists in knowledge of the distribution of woodland caribou on the AOSERP study area, and
2. A major gap exists in knowledge of the density of woodland caribou in various portions of the AOSERP study area.

A research proposal has been included in this report to provide data relevant to these knowledge gaps.

If data on the distribution and density of woodland caribou indicate that populations exist in portions of the AOSERP study area where they would be subject to the effects of oil sands development, then two other major data gaps would exist and remain to be filled before documentation and assessment of the resulting impacts could be completed:

1. A major data gap exists in knowledge of the seasonal level of use of each habitat type on the AOSERP study area; and
2. A major data gap exists in knowledge of the reactions of woodland caribou to sensory disturbances and the sphere of influence of the various types of sensory disturbances.

Research proposals concerning these data gaps have been deferred pending data on the distribution and density of the woodland caribou on the AOSERP study area.

9. WOLF

Population studies of wolves began in October 1975 in the Swan Hills of central Alberta. Techniques were developed for conducting wolf and prey base research, including radio-tracking of individuals and scat analysis, which were then applied to research conducted on the AOSERP study area in northeastern Alberta, starting in March 1976. Research efforts were terminated during the fall of 1976 in the Swan Hills, while they continued until December 1977 in the AOSERP area (Fuller and Keith in prep. a, c).

The specific objectives of these investigations were to determine wolf densities, distribution and movements relative to both moose and woodland caribou populations, rates and principal determinants of natality and mortality, food habits of wolves, and their predation rate on the large ungulates. The stated purpose was to quantify wolf-ungulate interactions for management (Fuller and Keith in prep. a).

The purpose of this critique is not to assess whether Fuller and Keith attained their objectives, but to evaluate the state of completion of baseline research in the AOSERP study area with respect to the data required to evaluate an assessment of the impact of large development projects on wolves. As with the moose and woodland caribou research, there are three types of biological data needed to document and assess the impact of oil sands development: seasonal population dispersion, the potential impacts of large development projects, and the population dynamics.

9.1 SEASONAL POPULATION DISPERSION

As discussed in the critiques of moose and woodland caribou research, there are three major facets of seasonal population dispersion which must be considered: distribution, habitat use, and movements. Because wolves prey upon ungulates that prefer to forage in certain types of habitat, they are indirectly associated with the habitats preferred by their prey. This renders an interpretation of seasonal population dispersion of wolves in a broader manner than for the moose and woodland caribou.

9.1.1 Distribution on the AOSERP Study Area

Wolves are known to occur throughout the AOSERP study area as evidenced by general observations and from trapper responses to a questionnaire (Fuller and Keith in prep. a, c). On the comparative study area, Swan Hills, wolves also appeared to be widely distributed (Fuller and Keith in prep. c). Wolves remain in the study areas throughout all seasons. Therefore, there is no requirement for additional data concerning distribution of wolves.

9.1.2 Habitat Use

As indicated in the literature review, there are considerable differences between summer and winter in food habits, foraging movements, territory size, and general activity of wolves, and in many cases these differences can be related to differences in the availability of prey within the pack territory (Banfield 1951; Jordan et al. 1967; Pimlott et al. 1969; Mech 1970; Van Ballenberghe et al. 1975; Voight et al. 1976; Mech 1977a, b, c; Theberge et al. 1978). In other words, the wolves respond to the habitat-related differences in the prey base. Furthermore, during the summer, wolves are tied to specific types of habitats which provide suitable pup-rearing areas--den sites and rendezvous sites (Joslin 1967; Kolenosky and Johnston 1967; Carbyn 1974). Therefore, any consideration of "habitat use" by wolves must deal with prey use, as well as specific habitat use for pup-rearing.

Knowledge of habitat and prey use is of cardinal importance for making any assessment of the impact of a large development on wolves because all such developments involve some degree of habitat disturbance, both in construction and operation of the development project itself, and in ancillary support developments. Not only must one know the natural variation in specific habitat use of the wolf, but one must also know the habitat use preferences of the wolves' prey for changes in habitat availability may affect prey availability, which has a direct effect upon the wolf population dependent on that prey base.

Investigations of the habitat use of wolves during the Swan Hills supplementary study were essentially nonexistent. No description of the habitats in which radio-collared wolves were located was provided nor was there any attempt to relate the occurrence of wolves to the habitat use of the prey. Food habits analysis was extremely cursory, and due to the inability of the researchers to locate any pup-rearing areas, the variability of the diet was not adequately examined. Both the Swan Hills and the AOSERP study area are composed largely of boreal mixed-woods, but due to the inadequate data gathering at the former location, the objective of developing a comparative approach (Fuller and Keith in prep. a, c) was not fulfilled. Therefore, the analysis of habitat use of wolves in the boreal mixedwood region in Alberta depends upon data collected in the AOSERP study area.

Even in the AOSERP study area, where research efforts were concentrated, little information was gathered on baseline habitat use and food habits. Most of the useful information on wolf population ecology was obtained from one pack out of 18 packs postulated for the entire AOSERP study area (Fuller and Keith in prep. a, c). Fuller and Keith report that radio-collared wolves' locations were mapped, distances between locations computed, and one rendezvous site located and examined. However, they do not present either a map of locations, or a table of distances moved within the pack territory, nor do they describe the rendezvous site, indicate its location, or the availability of such sites within the pack territory.

Spot locations obtained using radio-tracking methods are useful for habitat analysis only if a large sample size is obtained which includes good representation from all periods of the day and throughout the year. During the winter, observations of wolf-killed moose and their locations in a pack territory would indicate the importance of certain localities as foraging areas for the wolves. For the purpose of establishing pack home range, it is adequate to obtain locations once daily, or even less frequently as Fuller and Keith (in prep. a) have done for one pack in the AOSERP study area. Regarding the locations of wolf-killed moose, Fuller and Keith (in prep. a) state that 81 percent of these occurred in lowland areas, despite substantial (40 percent to 61 percent) distribution of moose in upland areas (Hauge et al. in prep.). This is a significant observation, but in order to fully relate wolf predation to moose distribution, a more detailed habitat analysis for locations of kills and living animals is required. It is inadequate simply to describe wolf radio-relocations as occurring in upland habitat types (49 percent), lowland habitat types (41 percent), and cutlines (10 percent) as Fuller and Keith (in prep. a) have done.

Investigations of the summer habitat use of wolves on the AOSERP study area were conducted only indirectly through scat analysis for diet. Only three pup-rearing areas were examined in the entire 25,000 km^2 study area; one den site and two rendezvous sites were examined. This is an inadequate sample to accurately reflect the diet and, hence, the dependence of the wolves upon prey utilizing different habitats. The abundance and availability of prey has been shown to largely determine the abundance of and health of wolves depending upon that prey base (see Section 5.2.6.2). It was also shown in the literature review that summer food habits are rather variable. With a biological parameter that exhibits considerable variation, such as diet, it is essential to sample the variability adequately in order to fully comprehend the interelationships involved.

The physical characteristics of den sites and rendezvous sites, as discussed in the literature review, indicate selection for certain types of areas for rearing of pups. The abundance and continuing availability of such locations are critical to the successful breeding of a wolf pack. These facets of pup-rearing sites were not examined by Fuller and Keith (in prep. a, c).

It is clear, then, that habitat use is an important facet of wolf population ecology. However, due to inadequate treatment in past studies, habitat use represents a major gap in the baseline knowledge of wolf populations in the AOSERP study area. Further investigation is required in order to complete the research needed to evaluate an assessment of the impact of oil sands development on wolves.

9.1.3 Movements

Wolves do not make long distance, *en masse* migrations except in areas where they follow ungulate prey that make extensive migrations (Cowan 1947; Kuyt 1972). In areas where the prey is relatively sedentary, as in the AOSERP study area, wolves generally remain within the pack territory, although movements inside the territory are quite extensive for hunting their ungulate prey (Mech 1966, 1970; Kolenosky and Johnston 1967). Pathways for hunting wolves consist of ridges, lake shores, river valleys, frozen watercourses, ungulate trails, cutlines, road verges and other man-made trails (Stenlund 1955; Mech 1970; Peters and Mech 1975).

A proliferation of man-made trails may change the pattern of wolf movements when hunting; however, as wolf movements do not commonly follow a predictable or regular pattern (Mech 1970) this is unlikely to be an area of concern. The selection of prey in specific habitats is of more concern and the end result of movements by wolf packs.

No data are presented on wolf movements in the AOSERP study area, except for mean daily distances travelled in winter (9.0 km) and mean distances between winter wolf kills (43 km) (Fuller and Keith in prep. a). Fuller and Keith document a high use of cutlines, as demonstrated by radio-relocations, which is in agreement with the general literature.

Movements are not a major area of concern with wolf packs that establish territories within which they conduct all their activities. Therefore, despite an absence of much information for the AOSERP study area wolves, only a minor gap exists in the baseline knowledge of wolf movements. As a result of investigations into habitat use by wolves, the salient points of wolf movement could be obtained to fill this minor gap and, consequently, aid in completion of research necessary for assessment of the impact of oil sands development on wolves.

9.2 POTENTIAL IMPACTS OF DEVELOPMENT PROJECTS

9.2.1 Sensory Disturbances

Little information has been published concerning the effects of sensory disturbances on wolves. Carbyn (1974) suggested that wolves may have initially tended to avoid busy highways in Jasper National Park since, despite the fact that elk and deer frequently travelled along road-edges, wolves rarely killed prey in these areas. However, wolves seem to have become accustomed to highways as the number of wolves scavenging at road kills along the major highways in Jasper National Park has increased in recent times. Wolf predation along highways was observed only along the highways with much less traffic in Jasper National Park (Carbyn 1974). Mech (1966) discovered that wolves readily become accustomed to the regular flight of a small plane above them.

Sensory disturbances are unlikely to directly effect a significant change in wolf behaviours. One exception is the effect of increased human activity near den sites; such activity and increased vehicular traffic have been associated with the desertion of three out of four traditional den sites found deserted in Jasper National Park (Carbyn 1974). Further, there may be an indirect effect upon wolves arising from sensory disturbances significantly disrupting distribution patterns of the prey. This indirect effect apparently has not been examined in wolf studies in general.

No investigation of the potential impact on wolf populations of sensory disturbances produced by oil sands development has been conducted (Fuller and Keith in prep. a, c). However, this represents only a minor gap in knowledge, since the concern is basically with the changes which may occur in the distribution of prey. This is comparable to the effect that habitat alterations might have on prey availability and is discussed under the topic of habitat alterations. Therefore, an extensive study of the direct effects of sensory disturbance upon wolves is probably not warranted.

9.2.2 Direct Mortality

There are two major mortality factors that may increase with development. One is accidental death, which may occur as a result of increased traffic on transport corridors in the development area or from other hazards. Wolves killed by vehicles are an uncommon mortality factor, the rate of which will depend upon the frequency and speed of vehicles on the roads, the frequency of road-killed prey animals to which the wolves are attracted for scavenging, and the density of the wolf population in the area. On 120 km of two major highways passing through Jasper National Park, less than one wolf was killed per year (Carbyn 1974). Such mortality levels are insignificant, although, because wolves are killed when scavenging, an increased dependence on such food sources may result in increased mortality.

The second major mortality factor that may change with development is human exploitation. An increased human population base may result in more wolves being taken. Over-exploitation resulting in strong population depression has been recorded for some Alaskan wolf populations (Rausch 1969; Stephenson 1978), but the wolf populations can return to former levels with proper management (Stephenson 1978). Fuller and Keith (in prep. a) did not report any accidental or road deaths of wolves, but did determine that trappers took between 15 and 20 wolves annually.

Management-related problems, such as potential increased exploitation of wolves, appear to fall outside of AOSERP's mandate. Further, since road deaths and other accidental mortalities appear to be generally uncommon, there is only a minor gap in the direct mortality information required to evaluate an assessment of the impact of oil sands development. Further study of direct mortality factors could be limited to documenting any occurrences of accidental deaths and identifying sources of mortality in the development area.

9.2.3 Habitat Alterations

As indicated above, this is probably the single, most important aspect of wolf population ecology that should be considered when examining the impact of development projects. This is also the area where least is known of the effects on a wolf population. With regard to oil sands development, the primary concern is with the complete removal of habitat as a result of open pit mining methods and tailings pond construction.

The direct result of such habitat removal is likely to be loss of prey to the packs whose territories are overlapping the development area. Such a loss may be in direct proportion to the density of the prey animal. It is known that wolves occur in low densities in areas with low ungulate prey densities (Banfield 1951; Stenlund 1955; Mech 1970), and also that wolf populations will decline if a major decline occurs in its primary ungulate prey population (Fau 1977; Mech 1977a, b, c). As inferred earlier, sensory disturbance of prey animals may produce results comparable to habitat alteration by frightening animals from suitable habitat. The end result to wolves is the same as habitat removal.

Habitat alteration may also bring about changes which increase interpack interaction. Social strife has been known to increase when wolves were forced, by a decline in prey, to trespass frequently (Mech 1977a, b, c). Mortality that occurs as a result of interpack strife is generally quite low (Mech 1970), but due to the social infrastructure of a wolf population an artificial disruption in prey density may affect mortality of wolves more heavily through social stress than through starvation.

On the other hand, habitat alterations which result in the production of seral vegetation communities would result in increased moose populations. Therefore, some forms of habitat alterations may also be beneficial to wolves.

A further concern with habitat alteration concerns the removal of traditional pup-rearing areas, which would clearly affect wolf packs to some degree. A wolf pack in any one year may use more than one den site for breeding and often uses several rendezvous sites for pup-rearing (Joslin 1967; Mech 1970). While a wolf pack may not be restricted to only single, critical sites, the abundance and availability of such important pup-rearing sites may be critical and possibly could be affected by habitat alteration.

As noted above, Fuller and Keith (in prep. a) do not deal at any length with habitat use by wolves. In order to fully assess the effect of habitat alteration, considerable effort must be expended upon analysis of habitat use and habitat availability. Therefore, there is a major gap in knowledge of the potential impact of oil sands development with regard to habitat alterations. Further study is needed to examine this aspect of the baseline knowledge required to evaluate an assessment of the impact of oil sands development on wolves.

9.3 POPULATION DYNAMICS

Baseline knowledge on the population dynamics of wolves is of primary importance to the evaluation of documented or potential impact. This information is required for comparison with the natural fluctuations with which wolf populations are able to cope. The major components of population dynamics are density, mortality, and natality.

9.3.1 Density

Fuller and Keith (in prep. c) determined the density for the Swan Hills wolf population to be 1 wolf per 65 km^2 and for the AOSERP study area to be 1 wolf per 100 km^2. Subsequent research (Fuller and Keith in prep. a) indicated that the density on the AOSERP study area was 1 wolf per 165 km^2. In neither report do Fuller and Keith provide adequate detail of their results, to permit an evaluation to be made of the accuracy of their density estimates. Observations of groups of wolves reveal that packs are often split up and that radio-tracking methods are often essential to obtain pack numbers (Van Ballenberghe et al. 1975; Mech 1977a, b, c). More widespread radio-tracking would be required to establish pack numbers and the territory sizes in the AOSERP study area.

On the basis of estimates by Fuller and Keith (in prep. c) and Hauge et al. (in prep.) the ratio of wolves to moose, the primary ungulate prey, is 1:100 in the Swan Hills and 1:53 in the overall AOSERP study area (1:32 for an intensively studied pack). The early estimate of 1:20 for the wolf:moose ratio on the AOSERP study area (Fuller and Keith in prep. c) was apparently too low. The less favourable ratio for the AOSERP study area wolf population reflects the larger territories occupied by packs and indicate that this population would be more severely affected by the impact of a large development project than would a population in Swan Hills.

Because of the unsupported documentation of most pack sizes and nearly all territory boundaries, it appears that there is a major gap in the knowledge of the true population density of wolves in the AOSERP study area. Therefore, further study is warranted to complete baseline research required for impact assessment.

9.3.2 Natality

The natality of wolves has been examined for a number of North American populations. The average litter size per adult female wolf ranges from 4.0 to 6.5 (Mech 1970). The proportion of females that successfully breeds in a population may vary from 59 percent in a population under natural control (Pimlott et al. 1969) to 89 percent in an exploited population (Rausch 1969). Wolves, therefore, have the reproductive potential to reproduce at a faster rate than their ungulate prey and will respond to exploitation by increasing the number of young. Age class data suggest that increased survival of pups (less *in utero* or early post-natal mortality) occurs in exploited populations (Mech 1970).

Fuller and Keith (in prep. a, c) obtained information on litters in three packs. Average litter size of young pups was 4.6. No further productivity data were gathered. However, because it has been shown that wolves generally have a substantial reproductive potential and have been able to rapidly reproduce after severe over-exploitation (Stephenson 1978), further investigation of natality is not needed on the AOSERP study area. Essentially no data gap exists for natality in so far as the need for baseline research to assess the impact of oil sands development has been satisfied through general literature.

9.3.3 Mortality

Factors of mortality, other than human exploitation, are widespread and should not change as a result of large development projects. Numerous factors have been recorded, such as disease, parasites, malnutrition, and hunting hazards (Mech 1970), but it has been impossible to provide much information on the proportion of a wolf population that dies from these various factors. Generally, there does not appear to be a large mortality rate caused by these natural mortality factors (Mech 1970).

Fuller and Keith (in prep. a, c) documented the death of a litter of three pups for unknown causes, one adult that apparently died of starvation, and another that was likely killed by a resident pack. In addition to these deaths, an average of 15 to 20 wolves were trapped annually on the AOSERP study area. Further deaths undoubtedly occur from natural mortality factors in the AOSERP study area, but they are likely to be minimal especially compared with the trapping mortality. The responsibility for management of wolf populations does not rest with AOSERP; any potential for overharvest of wolves resulting from increased access or human populations could be easily mitigated by adoption of an appropriate management plan by the responsible government agency. Therefore, since we do not believe that AOSERP has a mandate to provide data for management purposes, no further research needs to be conducted on this topic. However, if AOSERP is required to provide the data needed for the management of wolf mortality which would result from the anticipated increase in access and human populations, then the existing data are not adequate and information concerning the following knowledge gaps is required: (1) the current levels of hunter harvest; (2) the anticipated increase in hunter harvest induced by oil sands developments; and (3) the harvestable surplus of wolf on the AOSERP study area. Further investigation of the mortality of wolves on the AOSERP study area is probably not necessary. Adequate knowledge is currently available from local and general literature concerning the mortality of wolves.

9.4 SUMMARY

In summary, we consider that the following data gaps exist and remain to be filled before a documentation and assessment of the impacts of oil sands developments on wolves could be completed:

1. Habitat use by wolves, specifically related to habitat and prey distribution, and to the nature of movements within pack territories;
2. Potential impact of development projects primarily through habitat alteration and secondarily through sensory disturbances upon prey as well as wolves, and through direct mortality; and
3. Population density, specifically pack sizes, territory sizes, and number of packs as they reflect upon population dynamics.

A proposal for studies which will provide data concerning each of these data gaps has been included in this report.

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11. AOSERP RESEARCH REPORTS

1.		AOSERP First Annual Report, 1975
2.	AF 4.1.1	Walleye and Goldeye Fisheries Investigations in the Peace-Athabasca Delta--1975
3.	HE 1.1.1	Structure of a Traditional Baseline Data System
4.	VE 2.2	A Preliminary Vegetation Survey of the Alberta Oil Sands Environmental Research Program Study Area
5.	HY 3.1	The Evaluation of Wastewaters from an Oil Sand Extraction Plant
6.		Housing for the North--The Stackwall System
7.	AF 3.1.1	A Synopsis of the Physical and Biological Limnology and Fisheries Programs within the Alberta Oil Sands Area
8.	AF 1.2.1	The Impact of Saline Waters upon Freshwater Biota (A Literature Review and Bibliography)
9.	ME 3.3	Preliminary Investigations into the Magnitude of Fog Occurrence and Associated Problems in the Oil Sands Area
10.	HE 2.1	Development of a Research Design Related to Archaeological Studies in the Athabasca Oil Sands Area
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15.	ME 3.4	A Climatology of Low Level Air Trajectories in the Alberta Oil Sands Area
16.	ME 1.6	The Feasibility of a Weather Radar near Fort McMurray, Alberta
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18.	HY 1.1	Interim Compilation of Stream Gauging Data to December 1976 for the Alberta Oil Sands Environmental Research Program
19.	ME 4.1	Calculations of Annual Averaged Sulphur Dioxide Concentrations at Ground Level in the AOSERP Study Area
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22.	HE 2.3	Maximization of Technical Training and Involvement of Area Manpower
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24.	ME 4.2.1	Air System Winter Field Study in the AOSERP Study Area, February 1977.
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35.	AF 4.9.1	The Effects of Sedimentation on the Aquatic Biota
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37.	HE 2.2.2	Community Studies: Fort McMurray, Anzac, Fort MacKay
38.	VE 7.1.1	Techniques for the Control of Small Mammals: A Review
39.	ME 1.0	The Climatology of the Alberta Oil Sands Environmental Research Program Study Area
40.	WS 3.3	Mixing Characteristics of the Athabasca River below Fort McMurray - Winter Conditions
41.	AF 3.5.1	Acute and Chronic Toxicity of Vanadium to Fish
42.	TF 1.1.4	Analysis of Fish Production Records for Registered Traplines in the AOSERP Study Area, 1970-75
43.	TF 6.1	A Socioeconomic Evaluation of the Recreational Fish and Wildlife Resources in Alberta, with Particular Reference to the AOSERP Study Area. Volume I: Summary and Conclusions
44.	VE 3.1	Interim Report on Symptomology and Threshold Levels of Air Pollutant Injury to Vegetation, 1975 to 1978
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46.	VE 3.4	Interim Report on Ecological Benchmarking and Biomonitoring for Detection of Air-Borne Pollutant
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59.	TF 3.1	Self-Aquatic Mammals. Annotated Bibliography
60.	WS 1.1.1	Synthesis of Surface Water Hydrology
61.	AF 4.5.2	An Intensive Study of the Fish Fauna of the Steepbank River Watershed of Northeastern Alberta.

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